CAPITOSAUROID LABYRINTHODONTS FROM THE TRIAS OF ENGLAND

by ROBERTA L. PATON

ABSTRACT. Amphibian remains from several 'Lower Keuper' Sandstone localities in England, including the holotype of *Cyclotosaurus stantonensis* (Woodward), are examined. Differences in patterns of skull ornamentation in mastodonsaurs and parotosaur/cyclotosaurs are discussed and it is suggested that these are of taxonomic value. The specimens fall into three groups, two of which are species of *Cyclotosaurus*, the other group representing a primitive mastodonsaur. Basic differences between mastodonsaurs and parotosaur/cyclotosaurs are discussed.

The complicated nomenclature of the English fossils is investigated and the valid names of the cyclotosaurs are shown to be *Cyclotosaurus leptognathus* (Owen), of which *C. stantonensis* (Woodward) is a subjective junior synonym, and *C. pachygnathus* (Owen). The valid name of the mastodonsaur is demonstrated to be *Mastodonsaurus lavisi* (Seeley). The phylogeny of the superfamily Capitosauroidea is discussed.

The significance of the vertebrate remains in the stratigraphic correlation of the 'Lower Keuper' Sandstone is considered; the degree of specialization of the labyrinthodonts suggests an early Ladinian (Middle Trias, Upper Muschelkalk) age for their horizon.

THE fossils forming the basis of this study are from Triassic rocks in Warwickshire (Coten End SP 288655, Cubbington SP 335685), Bromsgrove (SP 960700) in Worcestershire, Stanton (SK 126462) in Staffordshire, and near Sidmouth (SY 105864) in Devonshire. All the specimens from Warwickshire were collected in the nineteenth century from quarries which have since been closed. Unfortunately there is no record of the actual collection of the specimens and therefore any association between them cannot be determined. They are all from horizons of approximately the same age which lie near the top of the 'Lower Keuper' Sandstone (Building Stones Formation of Warrington 1970) just below its junction with the Waterstones Formation.

The first major work on the English Triassic labyrinthodonts was published in 1842 by Owen who described and figured five species of labyrinthodont: *Labyrinthodon jaegeri* which was based upon two casts of portions of lower jaws, the originals having been lost; *L. ventricosus* based upon a single tooth; *L. scutulatus* based on a specimen showing a collection of bones of what is now recognized as a small lepidosaur; *L. pachygnathus*; and *L. leptognathus*. Some specimens referred to the latter two species were also reptilian, but others considered here are definitely labyrinthodont.

Miall (1874) described further discoveries from Warwickshire, assigning some specimens to a new genus and species, *Diadetognathus varvicensis*, and also commenting upon Owen's memoir pointing out the reptilian specimens and separating the two verified labyrinthodont species into different genera: *Mastodonsaurus pachygnathus* and *Labyrinthodon leptognathus*. Since 1874 the fragmentary labyrinthodonts in Warwick County Museum have not been studied.

Seeley (1876) described a labyrinthodont lower jaw from Sidmouth and assigned it to a new species, *L. lavisi*. He defended Owen's original designation of specimens into species of *Labyrinthodon*. Rather unfortunately he also refuted a suggestion

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that the labyrinthodonts were amphibian, maintaining that they were definitely reptilian showing resemblances to the Teleosauria and marine Chelonia.

Wills (1915) redescribed the lower jaws including *L. lavisi* and material from Warwickshire in the British Museum (Nat. Hist.) and the Geological Survey. Fragments of English Triassic labyrinthodonts are also present in the Sedgwick Museum and in the collection of the Department of Geology, Birmingham University. The complete skull of *Cyclotosaurus stantonensis* (Woodward) is from approximately the same horizon as the Warwickshire specimens.

As a group the 'capitosaurs' were among the earliest amphibians discovered; *Mastodonsaurus 'giganteus'* (*M. jaegeri*) from the Lettenkohle of Gaildorf in Germany was the first labyrinthodont to be described (Jaeger 1828). Since then, many new genera and species have been discovered and anatomical studies have been made by Huene (1922, 1932), Nilsson (1943, 1944), Watson (1919, 1926, 1951, 1958, 1962), and Romer (1947). Watson (1962) discussed various evolutionary trends in the group, e.g. progressive closure of the otic notch; progressive chondrification especially noticeable in the neurocranium and limb bones; an increase in dorso-ventral flattening of the skull (he suggested that there were two Upper Triassic lineages, one high-skulled and the other low-skulled); and an increase in size.

Welles and Cosgriff (1965) completely revised the group excluding *Mastodonsaurus* from the family Capitosauridae to which they assigned three genera: *Parotosaurus*, *Paracyclotosaurus*, and *Cyclotosaurus* with a much reduced number of species in the first and last genera. They commented briefly upon the English remains but decided that the only valid English capitosaur was *Cyclotosaurus stantonensis*. Recently, several new species have been described by Konzhukova (1965), Bonaparte (1963), Heyler (1969), Chowdhury (1970), Howie (1970), and Ortlam (1970).

'Capitosaurs' are known only from the basal Lower Trias to the Upper Keuper. They vary widely in size, the smallest being a skull 70 mm long from the Lower Trias of Queensland, and the largest being skulls of *C. hemprichi* (about 700 mm) and *Mastodonsaurus jaegeri* (*M. giganteus* of early authors) (about 800 mm). Undescribed fragments of skulls from East Africa in the collections of the British Museum (Nat. Hist.) and the Museum of Zoology, Cambridge University show that much larger skulls did occur; possibly as long as 1700 mm.

The labyrinthodont collection in Warwick County Museum contains many specimens but only those few which can be identified with reasonable certainty are included here. The rest of the specimens are on the whole very small and extremely fragmentary. Considerable difficulty was experienced with those described as very few show similar areas of the skull and so detailed comparisons between many of them were impossible.

Abbreviations preceding specimen numbers. Gz, Warwick County Museum; SM, Sedgwick Museum; R, British Museum (Natural History); GSM, Geological Survey Museum; BSp, uncatalogued specimens from the Geology Department, Birmingham University.

Abbreviations.

A	angular	C	coronoid
ant. pal. vac.	anterior palatal vacuity	clm. m.	cleidomastoideus muscle attachment area
ART	articular		
BO	basioccipital	D	dentary

ECT	ectopterygoid	p.q.f.	paraquadrate foramen
EO	exoccipital	PRA	prearticular
F	frontal	PRF	prefrontal
J	jugal	PSP	parasphenoid
L	lachrymal	PT	pterygoid
l.l.g.	lateral line groove	Q	quadrate
MX	maxilla	q. boss	quadrate boss
N	nasal	QJ	quadratojugal
obl. r.	crista obliqua	SA	surangular
P	parietal	SQ	squamosal
PF	postfrontal	ST	supratemporal
pin. f.	pineal foramen	T	tabular
PL	palatine	V	vomer
PMX	premaxilla	vag.(X) f.	foramen for vagus (tenth) nerve
PO	postorbital		
PP	postparietal	v.c.d.	vena capitis dorsalis

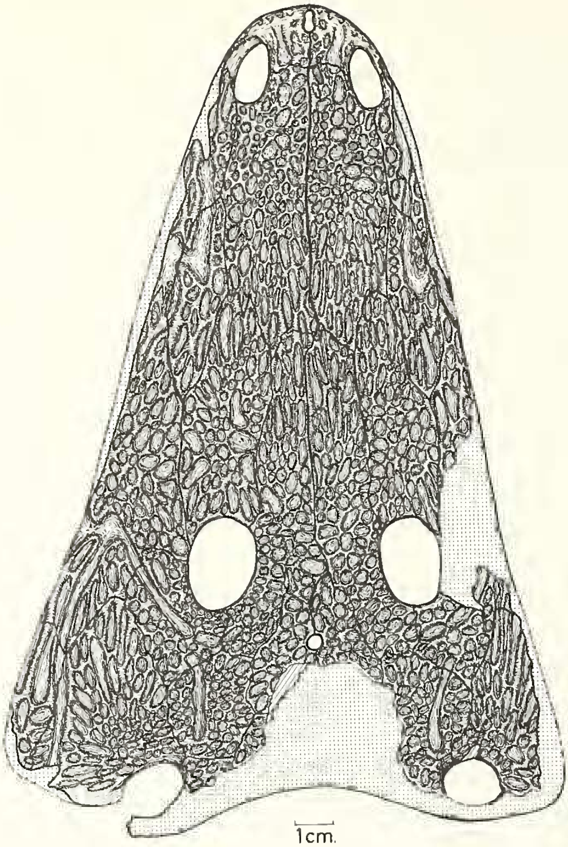
Cyclotosaurus leptognathus, specimen R 3174

Until now, this specimen has been known as *Cyclotosaurus stantonensis*. However, several of the fragmentary skull specimens from Warwickshire described in the following section are, for reasons discussed below (p. 264), believed to be conspecific with *C. stantonensis*. One of these specimens, Gz 38, was first described and figured by Owen (1842) as *Labyrinthodon leptognathus*. *Labyrinthodon* is a junior synonym of *Mastodonsaurus*. The trivial name *leptognathus* antedates *stantonensis* and so the correct name for the species including R 3174, is *Cyclotosaurus leptognathus*. This is explained below (p. 280).

The specimen R 3174 is from the 'Lower Keuper' Sandstone of Stanton in Staffordshire, its exact stratigraphical horizon being unknown. Its existence was first noted by Ward (1900) and it was more fully described by Woodward (1904) as *Capitosaurus stantonensis*. Zittel (1911) transferred the species to *Cyclotosaurus* and most authors since have agreed with this. Watson (1958), however, suggested that it should be called *Procyclotosaurus* on the basis of the deep skull, short exoccipital/pterygoid suture, and the retention of the crista obliqua on the pterygoid, and further suggested that it was a member of his high-skulled lineage not closely related to other cyclotosaurs. Welles and Cosgriff (1965) considered the division into low- and high-skulled forms invalid and returned the species to *Cyclotosaurus*, agreeing, however, that it seemed primitive and aberrant.

The specimen is in two parts, the one previously illustrated and discussed being the part with the well-preserved occiput, some of the palate, and the ventral impression of the cranial bones. The hitherto undescribed counterpart showed the underside of the cranial bones, the dorsal surface being embedded in a thick block of hard sandstone. Only a few sutures on the posterior part of the skull could be traced with certainty, some of those indicated by Woodward (1904) being incorrect. Very little useful comparison with other species showing the dorsal skull roof was thus possible. Preparation of this part of the specimen was carried out after the underside of the cranial bones had been embedded in Plaster of Paris; and the specimen was completely cleared of the matrix, a coarse, hard, pale-coloured sandstone stained with haematite close to the bone.

From this part, and the fragments of bone adhering to the counterpart, the



TEXT-FIG. 1. Specimen R 3174, skull roof as recently prepared.

complete skull roof can be reconstructed. The specimen is virtually undistorted, the left side being more complete than the right, much of which adheres to the figured part of the specimen.

The sutures on the skull are very clear and there can be no doubt about their positions. In fully adult labyrinthodonts, zones of intensive growth are visible as areas where the normal pits in the ornamentation are elongated into troughs (Bystrow 1935). In capitosaurs these zones are located anterior to the orbits at the prefrontal/frontal/nasal sutures, and postero-lateral to the orbits at the quadratojugal/jugal/squamosal sutures. In R 3174 the zones are present but not pronounced. This, and the open nature of the sutures, indicates that the skull is that of a young adult. Bystrow and Efremov (1940) studied age changes in *Benthosuchus sushkini* and from their data it can be predicted that with increasing age the skull would become larger

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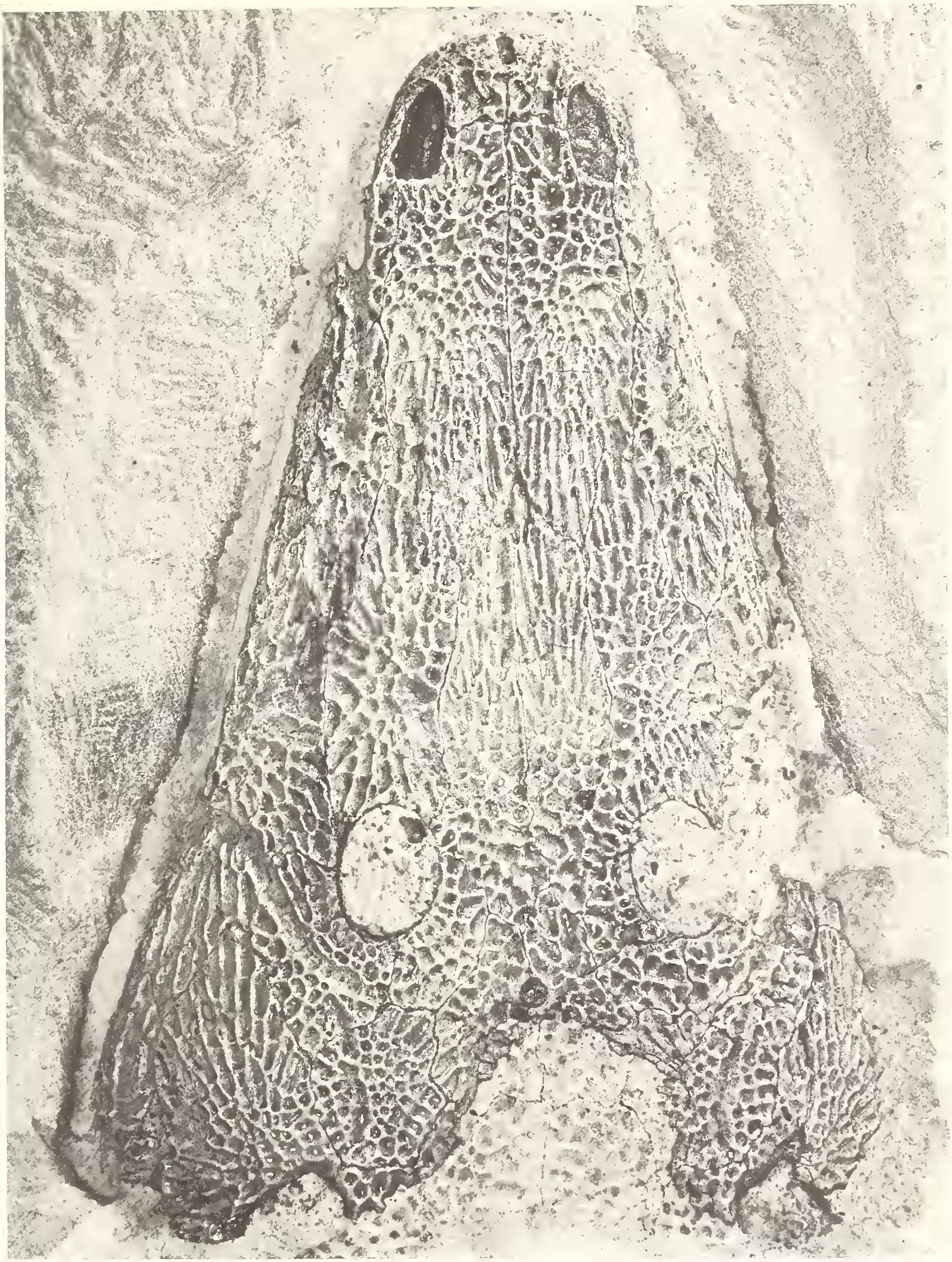
EXPLANATION OF PLATE 35

Specimen R 3174, *Cyclotosaurus leptognathus*, skull roof.



PATON, *Cyclotosaurus*

and broader; the orbits relatively smaller and more laterally placed (thus making it more typically cyclotosaurid); the pineal foramen would be relatively further behind the orbits; the occiput would be relatively shallower; and the posterior edge of the skull roof more concave.

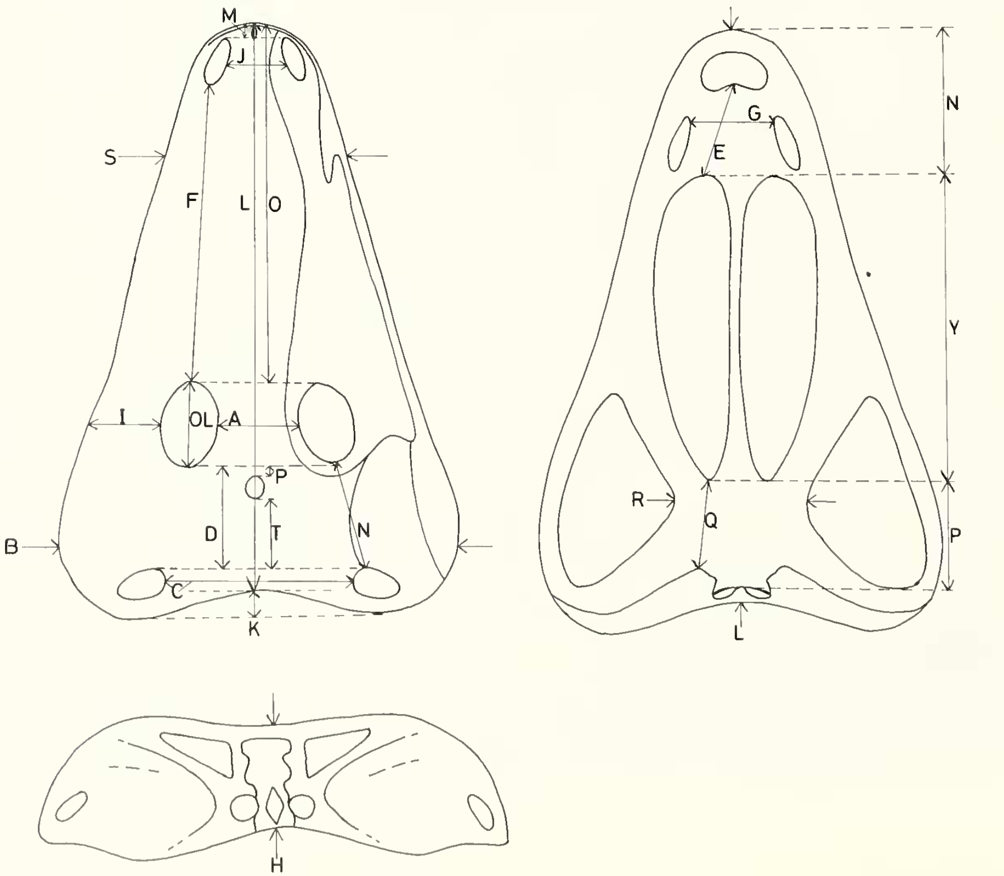
The ornamentation consists of wide, deep pits separated by high, narrow ridges which nowhere exceed the diameter of the pits. The lateral line grooves are only obvious in two places: the lachrymal flexure of the suborbital groove; and the supra-orbital groove on the postorbital, continuing into the jugal groove on the jugal and quadratojugal. These two areas of the grooves are those visible in all capitosaurs where the dorsal surface of the skull roof is preserved. The other grooves can be traced as slightly widened pits connected by lower ridges.

Measurements (in mm) *of specimen* R 3174 (see diagram):

B = 167	O = 137	A = 32	K = 13	G = 31	R = 61
L = 208	F = 110	D = 48	Y = 112	E = 16	H = 30
M = 12	S = 72	N = 41	T = 29	P = 7 skull roof	
J = 21	I = 38	C = 67	OL = 23	P = 32 palate	

Indices used by Welles and Cosgriff (1965):

B:L = 80	H:B = 22	C:L = 32	A:C = 48	P:C = 10·5	T:C = 43
S:L = 35	A:L = 15	A:OL = 75	N:C = 61	K:C = 19	



When the skull is viewed in profile, it is noticeably 'dish-faced' and this is not due to crushing. The skull thus has a very crocodilian appearance as both orbits and, to a lesser extent, the nares are situated above the level of the surrounding areas of the skull. Most capitosaurs have this appearance but it is particularly pronounced in this specimen.

Skull roof (text-figs. 1, 3A; Plate 35). The general plan of the skull roof is similar to that of typical members of the Capitosauridae, and this can be seen in the text-figures and plates. There are, however, one or two features of interest. An oval premaxillary foramen is present at the tip of the snout—this was probably present in all capitosaurs but can only be seen in well-preserved specimens. This foramen was probably connected with the anterior palatal vacuity and these may have been openings for a large intermaxillary gland which produced mucus as in modern Amphibia. The anterior commissure of the lateral line system can be seen running parallel with, and close to, the anterior edge of the snout on the premaxillae. No ornament is present here but the position of the commissure is marked by a series of nerve foramina. The jugal forms only a very small (5 mm) portion of the orbital border, being excluded mainly by the anterior expansion of the postorbital. The otic notches are impressions on both skull and counterpart and were obviously closed. They were pear shaped. The posterior edge of the left squamosal has a small, unornamented shelf which would be overlapped by the distal end of the tabular. Impressions indicate that the post-otic bar of the tabular was antero-posteriorly unexpanded unlike that of cyclotosaurs, and parotosaurs with semi-closed otic notches generally.

The palate and occiput are described from the already prepared part of the specimen which remained in the British Museum (Nat. Hist.). Some matrix adhering to the occiput tends to be misleading and the palate is incompletely exposed. Several features of interest can be seen.

Palate (text-fig. 4). On the right side, the base of the last premaxillary tooth is visible. It and the adjacent socket appear to be larger than the following maxillary teeth. This unusual condition will also be noted in specimen Gz 38. Most of the parasphenoid can be seen in ventral view although the cultriform process is damaged. The narrow central portion of this is sharply keeled ventrally. The basal plate of the parasphenoid is wide and short and the parasphenoid/pterygoid suture is short—these are both primitive features. The palatal ramus of the pterygoid is deeply concave ventrally and this surface is slightly sculptured as in *Parotosaurus nasutus*. On the left side the anterior face of the quadrate ramus of the pterygoid is exposed ventrally and shows a roughened area presumably for articulation with the hamate process of the prearticular.

Occiput (text-figs. 2 and 3B). The processus lamellosus of the exoccipital can be seen and below this at the base of the dorsal process of the exoccipital, a small, medially directed processus basalis is visible separating the partially ossified basioccipital from the foramen magnum. The crista basioccipitalis can be seen. The ridge for the attachment of the cleidomastoideus muscle (Howie 1970) is present on the ventral process of the tabular. The position of insertion of some of the occipital muscles is visible on the thickened upper edge of the triangular post-temporal fossa.

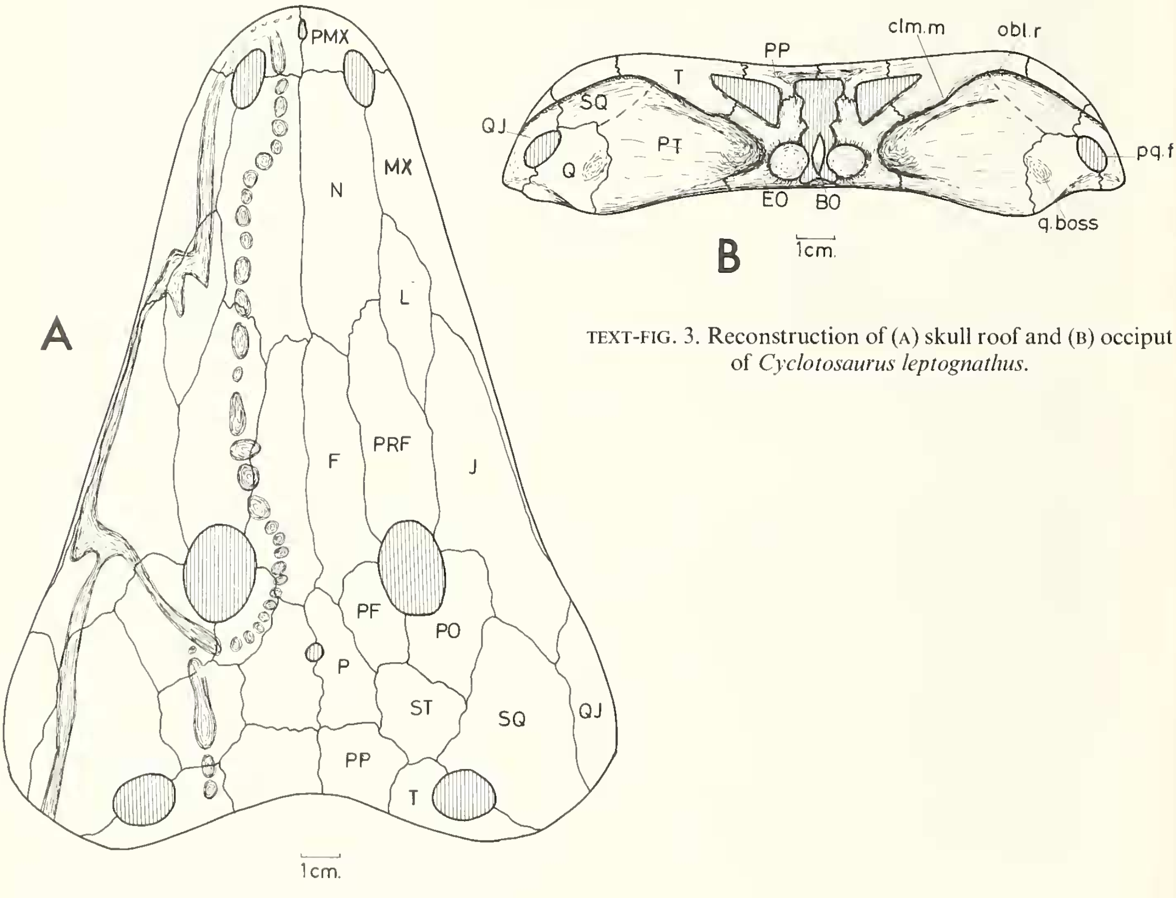
The condyle faces postero-ventro-medially. Its surface is roughened and was covered in life by a cap of cartilage supported by the slight frill of smoother bone around the edge of the condyle. The stapes is not preserved. Posteriorly the quadrate ramus of the pterygoid forms a lateral vertical wing of bone. This has a slightly roughened surface and dorsally shows traces of a slight crista obliqua—not a strong one as previously thought. A large quadrate boss is present on the pterygoid and quadrate just above the inner part of the quadrate condyle. The paraquadrate foramen is very long and is situated in the quadrate/quadratojugal suture. It is internally subdivided into several subforamina. Its long axis is parallel to the lateral occipital border formed by the quadratojugal.

No braincase or otic ossifications other than those mentioned above could be seen.

Primitive features of R 3174: 1, The basal plate of the parasphenoid is wide and short. 2, The parasphenoid/pterygoid suture is short. 3, The choanae are oval. 4, The snout is pointed. 5, The skull is high.

Aberrant features of R 3174: 1, The post-otic bar of the tabular is narrow. 2, The jugal is nearly excluded from the orbit. 3, The last premaxillary tooth and its adjacent socket are enlarged.

TEXT-FIG. 2. Specimen R 3174, *Cyclotosaurus leptognathus*, occiput.

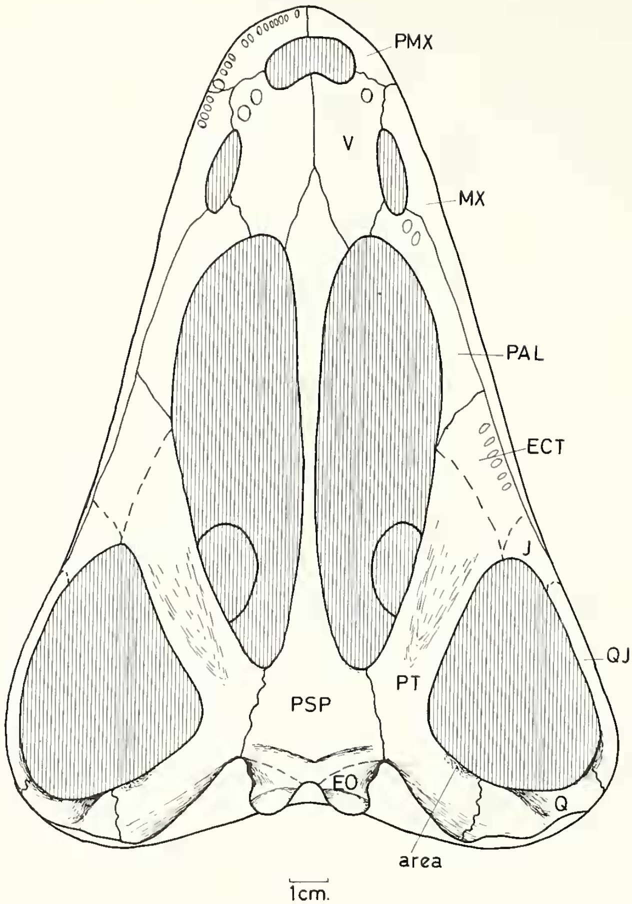


TEXT-FIG. 3. Reconstruction of (A) skull roof and (B) occiput of *Cyclotosaurus leptognathus*.

EXPLANATION OF PLATE 36

Specimen R 3174, *Cyclotosaurus leptognathus*, dorsal surface of counterpart.

PATON, *Cyclotosaurus*



TEXT-FIG. 4. Reconstruction of palate of *Cyclotosaurus leptognathus*.

Relationships of R 3174. As the otic notch is closed, R 3174 is a cyclotosaur, albeit a primitive and aberrant one. It seems to me that there is a strong possibility that the genus *Cyclotosaurus* is in fact a polyphyletic group united by the common feature of the closed otic notch which distinguishes them from parotosaurs. However, at present there is insufficient evidence to separate the members of the group generically and it is therefore convenient to retain them all in the genus *Cyclotosaurus*. Thus R 3174 is not here placed in a separate genus as it was by Watson (1958). One of the features which distinguished his genus *Procyclotosaurus* was the presence of a strong crista obliqua on the pterygoid. As Welles and Cosgriff (1965, p. 42) point out, however, the crista obliqua is present in most capitosaurs, its absence being merely an accident of preservation. In any case, the crista obliqua in this specimen is only slightly developed.

Fragmentary skull specimens

Identification of skull fragments

A visit to Ludwigsburg and Tübingen allowed study of the holotypes of *Mastodonsaurus jaegeri* Meyer (1844) from the Lettenkohle of Gaildorf, *Cyclotosaurus posthumus* Fraas (1913) from the Stubensandstein of Pffaffenhofen in Bavaria, *C. mordax* Fraas (1913) from the Stubensandstein of Pfaffenhofen, and *C. robustus* (Quenstedt) Fraas (1889) from the Schilfsandstein north of Stuttgart. Other material of *C. robustus* and *Mastodonsaurus jaegeri* was examined, in particular a very well-preserved but fragmentary skull of the latter.

The holotype and only skull of *Cyclotosaurus posthumus* is not complete as has been thought. The anterior part of the cranium and palate has been modelled in plaster. This area can be clearly seen in Fraas's (1913) plates as the unornamented part of the snout and a corresponding area of the palate. Plaster is also responsible for the unusual drop-shaped orbits of *Mastodonsaurus jaegeri* shown in all reconstructions. The holotype has been broken across the frontals just posterior to the prefrontal/frontal suture, and this break has been repaired with plaster which has been allowed to bulge into the orbits. These should be completely oval as are those of other specimens of the species. It should also be noted that the otic notches of the holotype of *M. jaegeri*, and of all other known mastodonsaurs, are definitely wide open. Fraas (1889, pl. 1) is slightly misleading in this respect as Welles (1947, p. 264) noticed.

As a result of the study of these specimens it is suggested that the genus *Mastodonsaurus* can be distinguished from the *Parotosaurus*/*Cyclotosaurus* lineage by the nature of the ornamentation and of the lateral line grooves. Different authors describe the ornamentation of labyrinthodonts in different terms. What might be coarse to one author is fine to another and thus it is virtually impossible to deduce from a description, diagram, or even from a photograph what the ornamentation is actually like. I have therefore confined my remarks to the admittedly limited number of specimens which I have seen myself. However, as these include the above holotypes and other specimens of these species, plus several other specimens of mastodonsaurs, parotosaurs, and cyclotosaurs, with casts of others, it is thought to be a reasonable conclusion. In all cases size has been taken into account.

In *Mastodonsaurus* (using data from the holotype, another specimen and fragments of *M. jaegeri*; fragments of *M. keuperinus*; and fragments of *Labyrinthodon jaegeri* from Germany which is obviously a mastodonsaur) the ornamentation consists of shallow pits separated by wide ridges which vary in height. The depth of the pits varies but in all places the ridges form the most prominent part of the ornamentation, often being as wide as the pits between them. This type of ornamentation appears to be present in juvenile specimens of *Benthosuchus* (Bystrow 1935, fig. 15). The lateral line grooves of *Mastodonsaurus* are very wide and shallow with respect to their width. This varies—they are slightly narrower posteriorly—but in all places the grooves are wider than the pits of the ornamentation.

The ornamentation of *Cyclotosaurus* consists of deep pits separated by high, narrow ridges; the pits thus form the most prominent part of the ornamentation and are deep all over the skull. The ridges are never as wide as the pits. The lateral line grooves are also deep and narrow. Only close to the external nares do they exceed the diameter of the pits, and then only by about one and a half times. Over the rest of the skull the grooves can only be distinguished from the pits by the fact that they are continuous. In places lower ridges do cross them and this may be why lateral line grooves are often incompletely figured in the skulls of cyclotosaurs. Specimens of large and small cyclotosaurs show this type of ornamentation and lateral line grooves, and that of parotosaurs, both adult and juvenile, is essentially the same.

Very few lower jaws were available for examination but it seems that their ornamentation is generally coarser than that on the corresponding skull roof. The lateral line grooves remain wide and shallow on the lower jaws of mastodonsaurs, and in cyclotosaurs they are narrow but more superficial than those of the skull roof.

No differences in the ornamentation of parotosaurs and cyclotosaurs could be detected, but this would be expected as the two genera are very closely related. The differences in ornamentation of these from mastodonsaurs corroborates the view that the two lineages are not closely related. Possibly mastodonsaurs evolved from primitive benthosuchids retaining some juvenile features such as the ornamentation and the large orbits.

Ornamentation is useful in the identification of some other labyrinthodonts, e.g. *Peltobatrachus* (Panchen 1959), *Plagiosaurus* (Nilsson 1937), *Dvinosaurus* (Amalitsky 1924); but these all possess very distinctive types of ornament. A survey of labyrinthodonts with the more normal reticulate sculpture would be interesting in case such small differences as those found between mastodonsaurs and parotosaur/cyclotosaurs are widespread. The ornamentation of *Parotosaurus* (*Stenotosaurus*) *semiclausus* will be discussed later.

Differences in ornamentation corresponding to those described above can be found in most of the specimens from the English Trias. That of R 3174 is typical of the cyclotosaurid type. It is noteworthy that the specimens identifiable by other means, e.g. Gz 20, the interorbital plate; Gz 14, the otic notch region; all confirm these differences. The specimens fall into three groups: a species of mastodonsaur, and two species of cyclotosaur.

The mastodonsaur specimens represent skull lengths of 400 to 600 mm. The skull had relatively large orbits, but not as large as those of *Mastodonsaurus jaegeri*. The species closest to the English one in relative orbital size seems to be *M. cappelensis* (see p. 266), of which one specimen was seen in Tübingen. The English species is probably later in age—*M. cappelensis* is from the Upper Bunter and is considered by Welles and Cosgriff (1965) to be a suitable ancestor for *M. jaegeri*. Possibly the English species is a little modified descendant of *M. cappelensis* or a closely related form. The material is thought to be sufficiently distinctive to allow a diagnosis of a new species of *Mastodonsaurus*—*M. lavisi*—to be made (see p. 282).

One of the species of *Cyclosaurus* is *C. leptognathus*. The snout Gz 38 is very similar indeed to that of R 3174. One unusual feature in both is the enlargement of the last premaxillary tooth and its adjacent socket. Gz 6 is also very similar to the same area in R 3174, the paraquadrate foramen being relatively very large in both specimens. Gz 11 is included here as it seems to come from a deep-skulled cyclotosaur. The lower jaw Gz 35 is slender and is considered to be the most likely type of jaw to be associated with a skull such as R 3174. Thus Gz 38, Gz 6, Gz 11, and Gz 35 indicate the presence in the 'Lower Keuper' Sandstone of a small, deep-skulled cyclotosaur with a primitive anterior palatal structure, unusual last premaxillary teeth, slender snout, and large paraquadrate foramina. All these characters agree closely with those in R 3174 and the specimens are therefore thought to be conspecific.

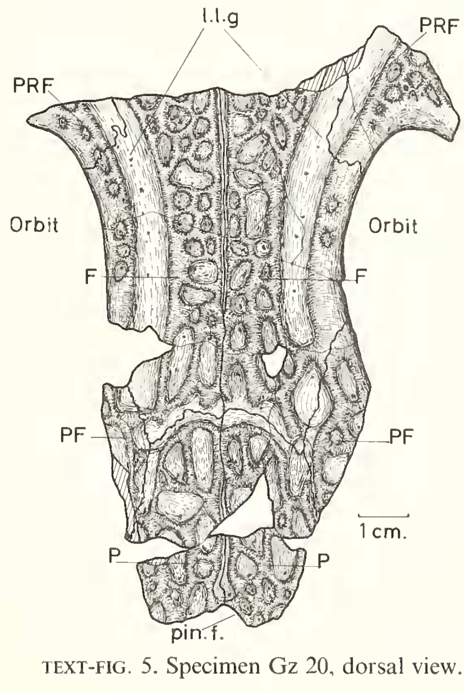
The other specimens attributed to the genus *Cyclotosaurus* apparently belong to a more typical cyclotosaur of moderate size with a shallow skull. Specimens Gz 14 and Gz 26 are typically cyclotosaurid with laterally elongated and distally expanded tabulars. They show differences in the shape of the tabular and in its relations to the surrounding bones, but these differences are only what would be expected from inter-individual variation. Wide variations in the positions of sutures and the relative sizes of different bones have been noted in species known from many specimens, e.g. *Benthosuchus sushkini* (Bystrow and Efremov 1940); *Buettneria bakeri* (Case 1932). In addition, Gz 13 is included here because of the shallowness of skull which it indicates, and Gz 36 because it too shows a shallow skull, and also because the anterior part of the palate shows a circular choana (a more advanced cyclotosaur character). GSM 27964 and BSp 2 are included here because they seem to be typical cyclotosaur lower jaws. The shape of the otic notch and its orientation, which varies in different species of cyclotosaurs, is very close to that of *Cyclotosaurus posthumus* and the tabulars appear to be similarly constructed in this species. No diagnosis is possible for these few fragments, but for ease of reference the species has been named *C. pachygnathus* (see p. 280).

The fragmentary specimens are here described grouped in the above three species:

1. Specimens attributed to *Mastodonsaurus lavisi*:

Specimen Gz 20 (text-fig. 5).

Identified by Miall (1874, pl. XXVI, fig. 1A) as the interorbital plate of *Mastodonsaurus pachygnathus*.



TEXT-FIG. 5. Specimen Gz 20, dorsal view.

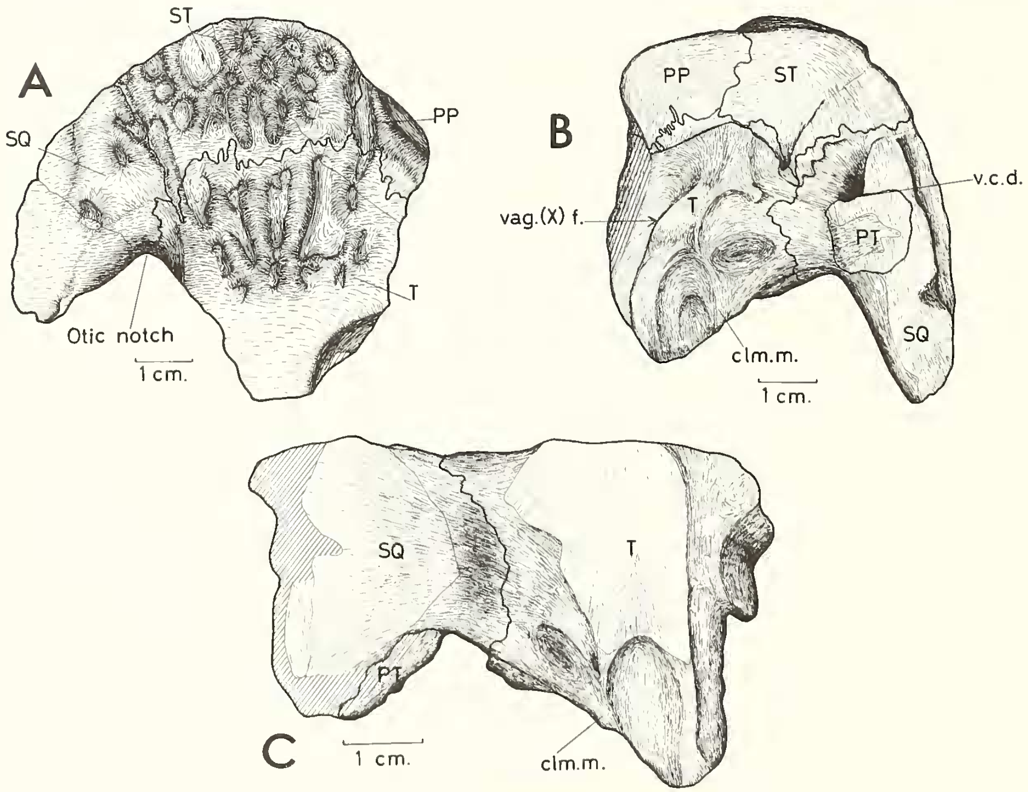
It is uncrushed. The reconstructed orbit is oval with the long axis almost antero-posterior and 57 mm long. The transverse axis is 31 mm. The lateral lines are very wide and deep and the ornamentation is of shallow pits separated by wide ridges. From Table 1 it can be seen that the only genus having a ratio of interorbital width: orbital length greater than 100% is *Mastodonsaurus*. Because of this, and the nature of the ornamentation, the specimen is assigned to this genus and is considered to be closest to *M. cappelensis*.

TABLE 1. Comparative ratios of orbit measurements in different species of capitosauroids.

	Interorbital width: orbital length (%)		Interorbital width: orbital length (%)
Specimen Gz 20	121	*C. ebrachensis*	62
Mastodonsaurus cappelensis	123	*C. hemprichi*	45
M. acuminatus	207	*Paracyclotosaurus davidi*	74
M. jaegeri	286	*Parotosaurus nasutus*	74
Cyclotosaurus robustus	81	*P. haughtoni*	78
C. leptognathus	75	*P. semiclausus*	76
C. posthumus	62	*P. brookvalensis*	85

Specimen Gz 9 (text-fig. 6).

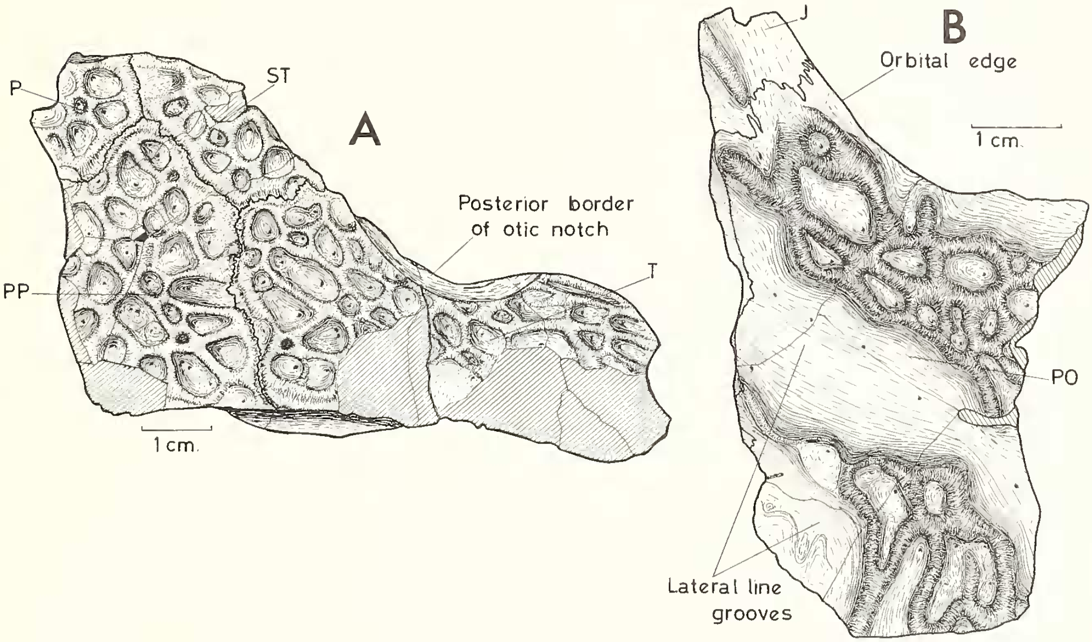
Identified by Miall (1874, pl. XXVI, fig. 2A, B, C) as a portion of the occipital border of *Mastodonsaurus* sp. It shows the left otic notch and tabular horn. The posterior face of the tabular shows the ridge and trough for the dorsal attachment of the cleidomastoideus muscle used in raising the head (Howie 1970),



TEXT-FIG. 6. Specimen Gz 9. A, dorsal view; B, ventral view; C, posterior view.

the other end being attached to the dorsal process of the clavicle. Below the wall of squamosal forming the otic notch a small fragment of the quadrate ramus of the pterygoid has been displaced anteriorly for 18 mm.

Although the specimen has been weathered, it is apparent that the otic notch was widely open, and the tabular horn resembles that of *M. jaegeri*. The ornamentation shows deep pits separated by low, wide ridges and for these reasons the specimen is assigned to the genus *Mastodonsaurus*.



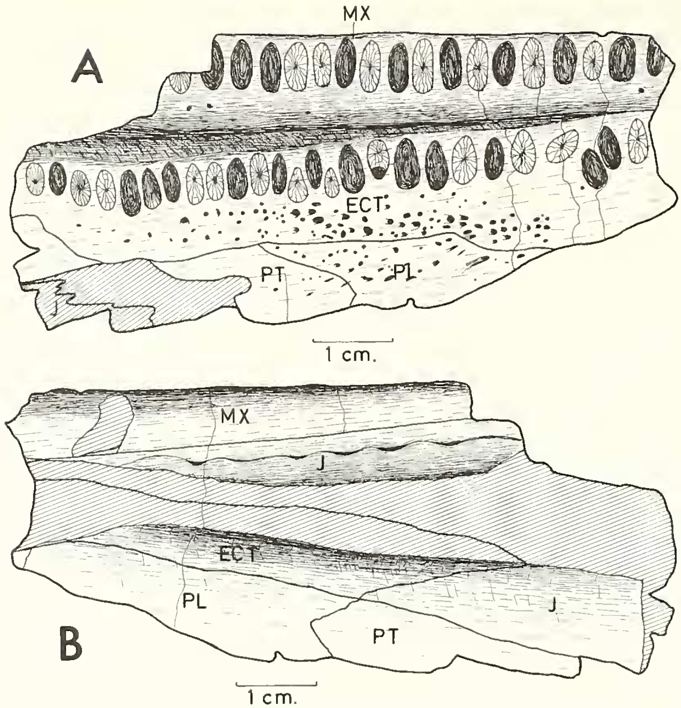
TEXT-FIG. 7. A, Specimen Gz 26, dorsal view; B, specimen Gz 1057, dorsal view.

Specimen Gz 1057 (text-fig. 7B).

Identified by Miall (1874, pl. XXVI, fig. 1B) as the left postorbital of *Mastodonsaurus* sp. It was figured in conjunction with Gz 20, but there is no record of any association between the two. It is the left postorbital with anteriorly, part of the jugal. The anastomosis of the supra- and infraorbital grooves is visible. The ornamentation is of deep pits separated by wide ridges. The orbit is large both relatively and absolutely, and the postorbital is unexpanded anteriorly. These features indicate that the specimen belongs to the genus *Mastodonsaurus*.

Specimen BSp 1 (text-fig. 8).

This is an unfigured specimen from the 'Keuper' Sandstone of Bromsgrove. It is part of the right upper jaw. The maxilla projects laterally as a wedge whose upper surface forms the base of a large and wide lateral line groove running in the jugal/maxillary suture. The ventral surface of the maxilla is separated from the palate by a step 8 mm deep. The external palatal element is the ectopterygoid. Internal to its tooth row, the bone is perforated by many small, posteriorly directed foramina which are probably for small blood vessels supplying the mucosa of the roof of the mouth which assisted in respiration. The extent of the other palatal bones is not great. The dorsal aspect of the specimen shows a small fragment of the dermal ornamentation 34 mm from the anterior end, indicating that only a small part of the bone is missing dorsally.



TEXT-FIG. 8. Specimen BSp 1. A, ventral view; B, dorsal view.

The estimated skull length of the animal is 500–550 mm, and the large and wide lateral line groove, the fragment of ornamentation showing a wide pit, and the antero-posteriorly compressed teeth indicate that it was a species of *Mastodonsaurus*.

Specimen SM 369 (text-fig. 13C).

Identified by Wills (1907) as the cranial bones of a labyrinthodont (?*Mastodonsaurus*). It is part of the posterior edge of the skull. The ornamentation consists of shallow pits and wide ridges. The skull length is estimated at between 500 and 600 mm and the posterior border of the skull is only slightly concave. The ornamentation suggests that it is from a mastodonsaur.

2. Specimens attributed to *Cyclotosaurus pachygnathus*:

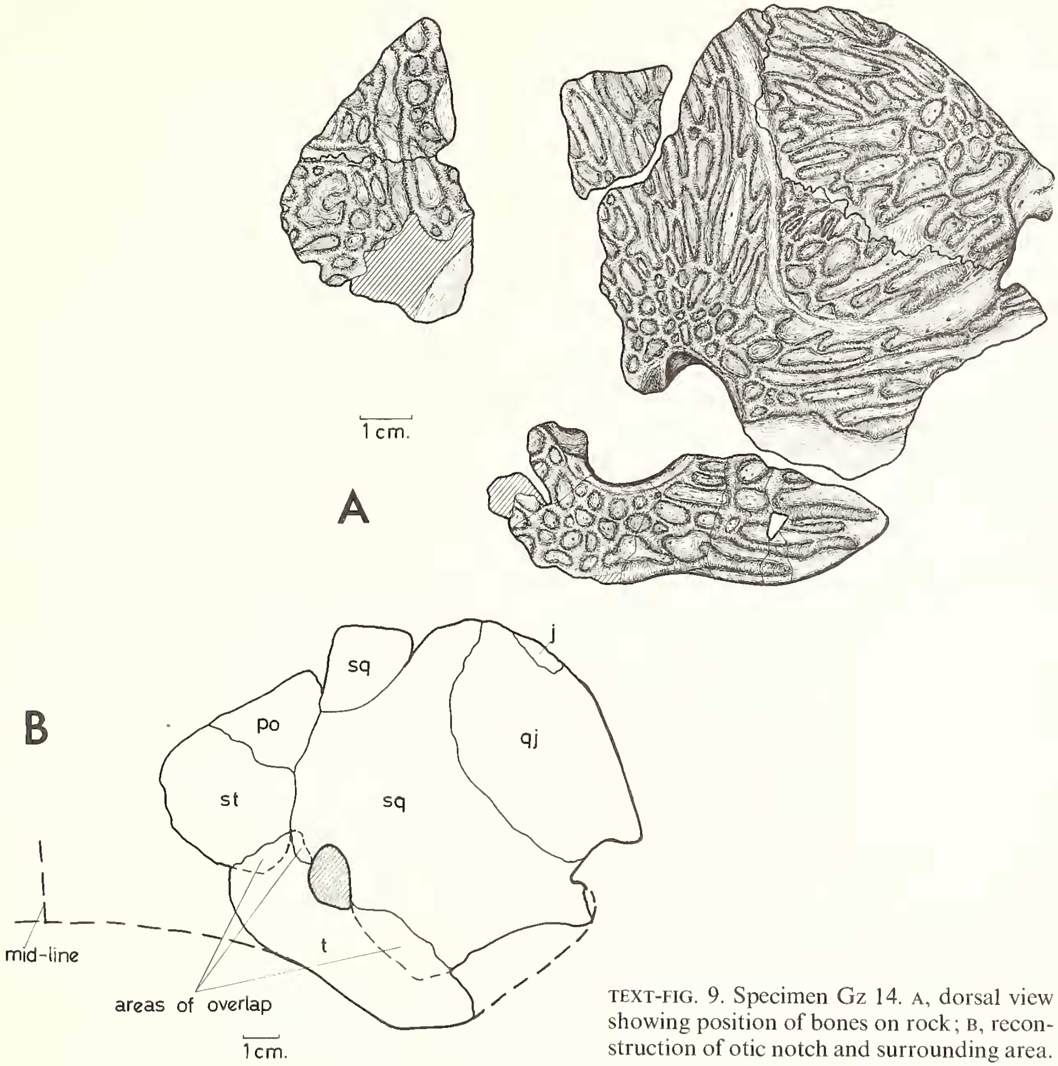
Specimen Gz 14 (text-fig. 9).

Figured, but not interpreted, by Owen (1842, pl. 46, figs. 6, 7) as *Labyrinthodon pachygnathus*. Miall (1874) correctly identified it as the right otic notch area but confused the otic notch and the postero-ventral corner of the skull. He also referred it to his new genus *Diadetognathus*. The three bone masses on the specimen are obviously closely related and their correct positions in relation to one another can be restored (text-fig. 9B).

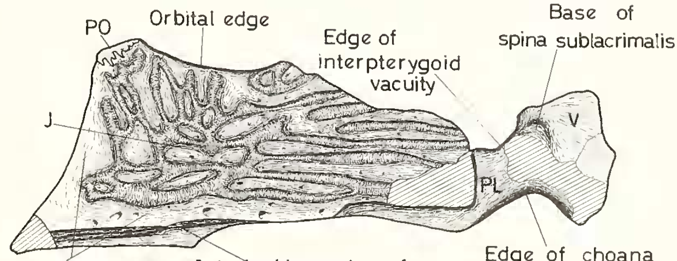
The otic notch in this specimen was completely closed as a result of the postero-lateral growth of the tabular and it must therefore belong to the genus *Cyclotosaurus*. The ornamentation, of deep pits separated by high, narrow ridges, confirms this.

Specimen Gz 36 (text-fig. 10).

Identified by Owen (1842, pl. 43, figs. 9, 10) as the left maxilla and intermaxilla with the palatal plate of *Labyrinthodon pachygnathus*. The ornamented part of the specimen is the right jugal. This is broken



TEXT-FIG. 9. Specimen Gz 14. A, dorsal view showing position of bones on rock; B, reconstruction of otic notch and surrounding area.



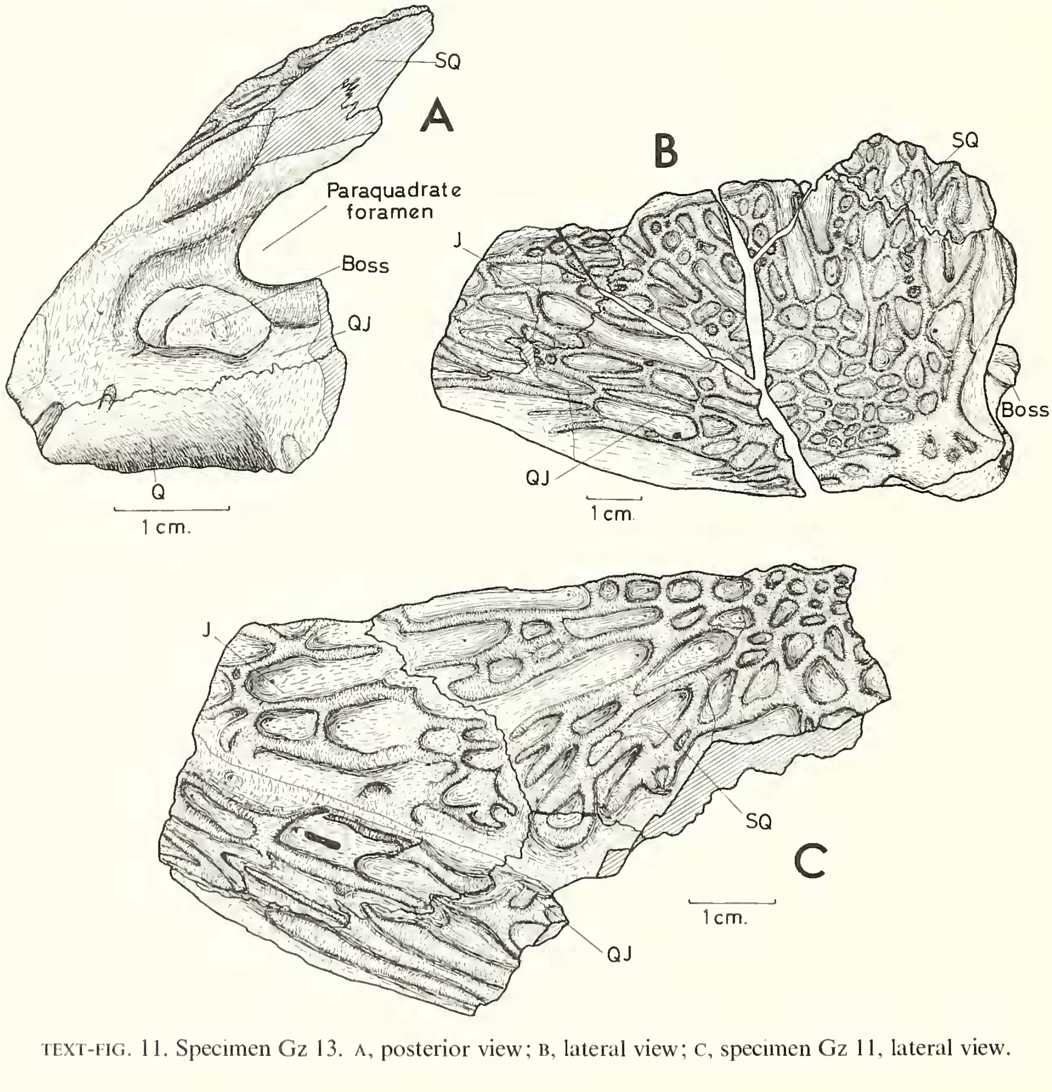
TEXT-FIG. 10. Specimen Gz 36, dorsal view.

34 mm from the anterior end revealing part of the underlying palate with portions of the right interpterygoid vacuity and the subcircular choana. Between the choana and the interpterygoid vacuity is the base of a ridge which may be the spina sublacrimalis, a posteriorly directed spine with a broad base on the palatine close to the choana. This was figured by Bystrow and Efremov (1940) in *Benthosuchus sushkini* but is not known in other capitosaurs, probably because the dorsal surface of the palate is very rarely exposed. The palatal element has been displaced posteriorly and twisted slightly clockwise.

The ornamentation consists of deep pits separated by high, narrow ridges. The animal apparently had a small orbit and these features suggest that it belonged to a cyclotosaur. It had a shallow skull.

Specimen Gz 13 (text-fig. 11A, B).

Identified by Miall (1874, pl. XXVII, fig. 1A, B) as the left postero-external angle of the skull of *Mastodonsaurus pachygnathus*. The ornamentation is of shallow pits and narrow ridges. Just ventral to the paraquadrate foramen and wholly on the quadratojugal, is a large oval projection. Its extreme lateral position shows that it cannot be the quadrate boss normally found close to the articulation. No similarly placed



TEXT-FIG. 11. Specimen Gz 13. A, posterior view; B, lateral view; C, specimen Gz 11, lateral view.

projection has been seen on other specimens and its position just above the lateral condyle must have inhibited the jaw mechanism. Possibly this lump is pathological in origin, the bone comprising it has an unusual surface texture not seen anywhere else, and the specimen's general appearance suggests that it came from an old animal. The condylar surface is roughened and was covered by cartilage in life. The estimated skull length is about 450 mm and the occiput was very shallow. The nature of the ornamentation suggests that it came from a cyclotosaur.

Specimen Gz 26 (text-fig. 7A).

Identified by Miall (1874, pl. XXVII, fig. 4A, B) as the epiotic and adjacent bones of ?*Mastodonsaurus*. It is almost the complete right tabular with parts of the surrounding bones. The ornamentation is of deep pits and high narrow ridges. The tabular is distally expanded. Some parotosaurs have otic notches which are almost closed and in these the tabular has a lateral extension like that of Gz 26. However, direct comparison shows that the extension in this specimen is relatively greater and therefore the otic notch was closed. Thus the specimen is from a cyclotosaur and the nature of the ornamentation confirms this.

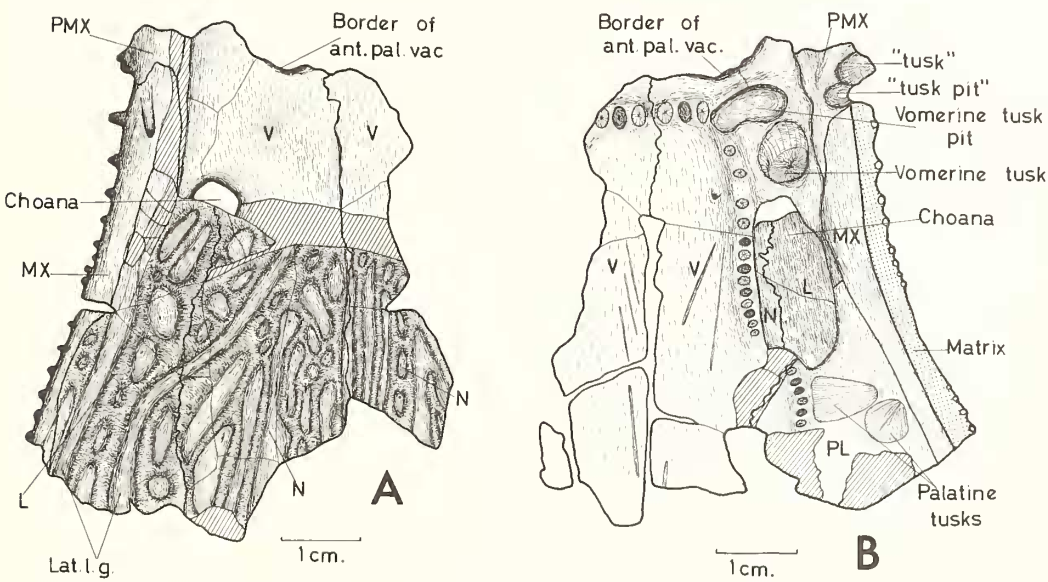
3. Specimens attributed to *Cyclotosaurus leptognathus*:

Specimen Gz 38 (text-fig. 12).

Identified by Owen (1842, pl. 43, figs. 1, 2, 3) as *Labyrinthodon leptognathus* and designated by Miall (1874) as type. It shows part of the snout from the posterior edge of the anterior palatal vacuity, to about the level of the anterior edge of the interpterygoid vacuities. Part of the right side is missing. The dorsal surface is flat and the specimen has been slightly crushed dorso-ventrally. The ornamentation is of small, deep pits and high ridges. There are two narrow and deep lateral line grooves.

The premaxilla is only preserved posteriorly and bears one large, antero-posteriorly flattened tooth broken 6 mm from its base which is 5×4 mm. It is followed by a large socket. The circular maxillary teeth are much smaller (2 mm diameter anteriorly) and are arranged as follows (I = tooth present; X = tooth absent):

Premax. / Max.
IX /IXIXIXIXIIIIXIXIXIXIXIXI
/ \
A B



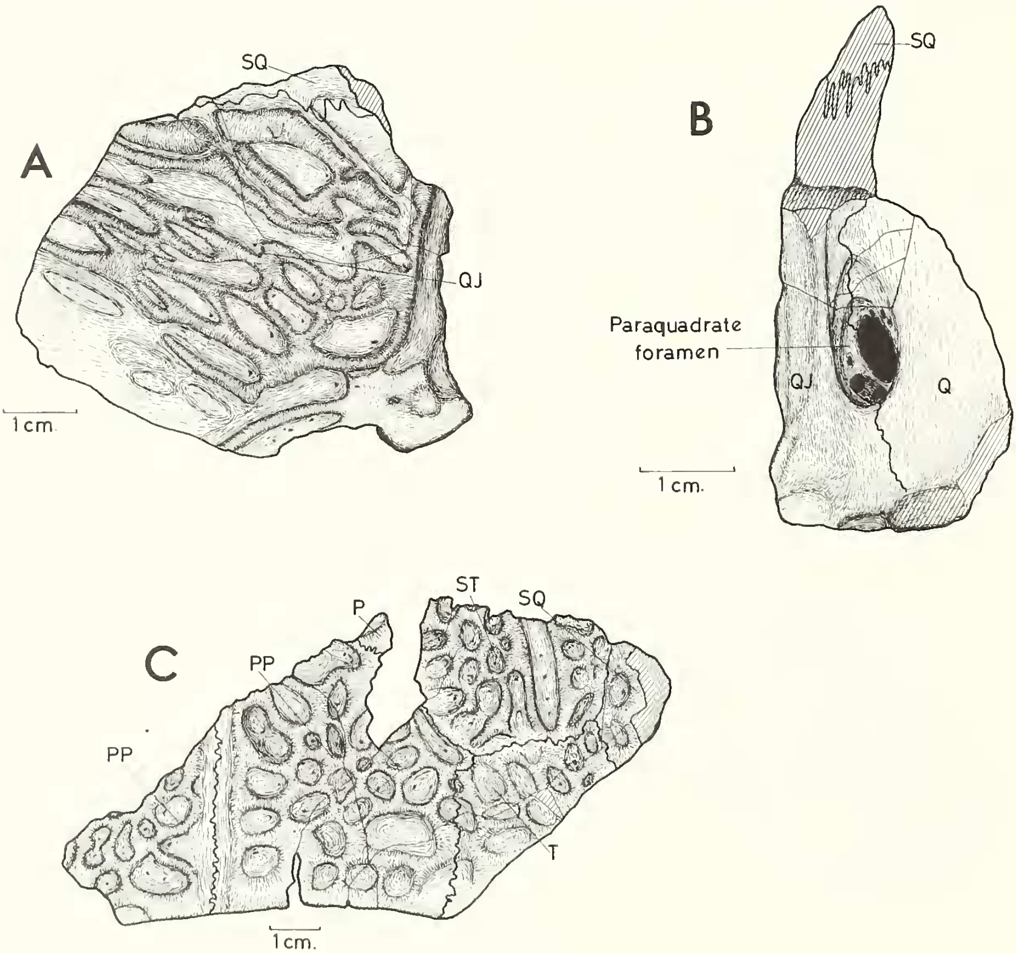
TEXT-FIG. 12. Specimen Gz 38. A, dorsal view; B, ventral view.

Thus, apart from the group of four adjacent teeth, alternating tooth replacement occurs. All the teeth except (B) are broken, many showing the pulp cavity. (B) is 3·5 mm long and had probably just erupted as the adjacent teeth are equally long but broken. All the teeth except (A) are firmly fused to the bone of the upper jaw. (A) however, a fairly large tooth, may have been loosening in the jaw prior to shedding.

Just lateral to the palatine tooth row are the crushed remains of two palatine tusks, the inner anterior one having been pressed down upon the outer one. The specimen belonged to an animal with a skull length of about 200 mm. Its shape shows that the snout was fairly pointed as in *Cyclotosaurus* '*stantonensis*', this shape being primitive for a cyclotosaur. It is assigned to the genus *Cyclotosaurus*, and its ornamentation confirms this.

Specimen Gz 6 (text-fig. 13A, B).

Identified by Owen (1842, pl. 43, fig. 11) as the anterior frontal of *Labyrinthodon pachygnathus.* Miall (1874) reidentified it correctly as part of the occipital region. It is part of the left postero-ventral corner of the skull. The ornamentation is of shallow, narrow pits and high ridges. Traces of a narrow, shallow lateral line groove are present; it is difficult to distinguish from the ornamentation. The paraquadrate foramen is large and oval; there are four small foramina in the outer rim and inside is a large dorsal foramen with



TEXT-FIG. 13. Specimen Gz 6. A, lateral view; B, posterior view; C, specimen SM 369, dorsal view.

two smaller ventral foramina and two or three accessory foramina. The quadrate/quadratojugal suture can be traced across the foramen.

The estimated skull length from the specimen is 300–400 mm. The paraquadrate foramen is very large, a feature which also occurs in R 3174. The specimen is thought to have come from a cyclotosaur with a deep skull.

Specimen Gz 11 (text-fig. 11C).

Identified by Miall (1874, pl. XXVII, fig. 2) as the right postero-external angle of the skull. However, he oriented it incorrectly and it is part of the left side just in front of the postero-ventral corner of the skull. The ornamentation is of fine pits and high ridges. There is a deep, narrow lateral line groove parallel to the lower edge and 22 mm above it. At the posterior edge of the specimen it appears to curve upwards following the broken edge which is probably the position of the squamosal/quadratojugal suture. Dorsally the bone thickens and the base of a downwardly projecting spur can be seen; this is presumably part of the dorsal support for the lateral wall of the braincase.

The specimen indicates a skull length of about 250 mm. The nature of the ornamentation and lateral line groove suggest it belongs to a cyclotosaur and the skull appears to have been deep.

Lower jaws

The general structure of capitosaur lower jaws is well known and need not be discussed here (see Romer 1947; Nilsson 1943, 1944; Wills 1915; Howie 1970). The specimens of lower jaws all conform to this general pattern. Lower jaws from Warwickshire are as follows:

Specimen Gz 15—*Mastodonsaurus pachygnathus* Miall, 1874, no. 6, pl. XXVI, fig. 3A, B. The posterior end of a right lower jaw from just in front of the anterior end of the adductor fossa. Identified here as *M. lavisi* (text-figs. 14A, 16A).

Specimen Gz 37—*Diadetognathus varvicensis* Miall, 1874, no. 9. Part of a right lower jaw showing the anterior part of the adductor fossa and the posterior part of the posterior Meckelian fossa. Identified here as *Mastodonsaurus lavisi* (text-fig. 14C).

Specimen Gz 35—*Diadetognathus varvicensis* Miall, 1874, no. 8, pl. XXVII, fig. 3A, B. The posterior end of a left lower jaw showing the same area as Gz 15. Here referred to *Cyclotosaurus leptognathus* (text-figs. 15A, 16C).

Specimen GSM 27964—*Mastodonsaurus jaegeri* Huxley, 1859; Wills, 1915, pl. 3. The posterior end of a left lower jaw from the middle of the adductor fossa. Here referred to *Cyclotosaurus pachygnathus* (text-figs. 15B, 17B).

Specimen Gz 27—*Labyrinthodon leptognathus*. Two small pieces of lower jaws, one the anterior part and the other a central part with a portion of the coronoid series. These are not considered further as the posterior part, only, of the lower jaw shows diagnostic features.

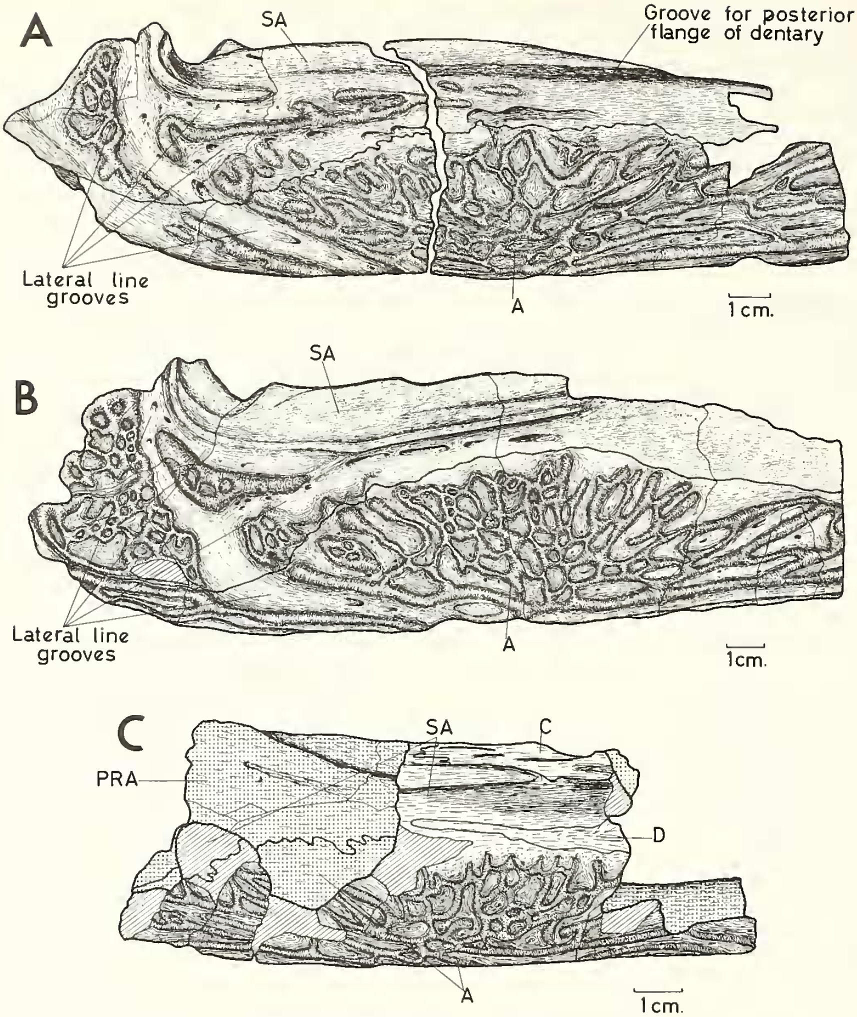
Several other fragments of lower jaws are in Warwick County Museum, but these are mainly the undiagnostic anterior parts, some of which were figured by Owen (1842). The following specimens come from quarries at Bromsgrove:

Specimen BSp 2—?*Diadetognathus* Wills, 1915, no. A, pl. 2, figs. A, B, C, D. The posterior end of a right lower jaw from the anterior end of the adductor fossa. Identified here as *Cyclotosaurus pachygnathus* (text-figs. 15C, 17A).

Specimen BSp 3—*Labyrinthodon leptognathus* Wills, 1915, no. B, pl. 2, figs. E, F, G. The anterior end of a left lower jaw. Not diagnostic.

The following specimens come from Sidmouth:

Specimen R 4215—*Labyrinthodon lavisi* Seeley, 1876, pl. XIX, figs. 1, 2, 3. The posterior end of a right lower jaw from the posterior Meckelian fossa. Identified here as *Mastodonsaurus lavisi* (text-figs. 14B, 16B).



TEXT-FIG. 14. A, specimen Gz 15, lateral view; B, specimen R 4215, lateral view (anterior part of specimen omitted); C, specimen Gz 37, lateral view.

Specimen R 331—*Mastodonsaurus*. A portion of a right lower jaw at the level of the adductor fossa. Referred here to *M. lavisi*.

Some specimens thus show the posterior ends of the lower jaws and can therefore be directly compared (Table 2). Specimens Gz 15 and Gz 35, although identical in size and area, show many differences as indicated in the following comparisons:

1, The specimens are of the same size but Gz 15 is much more massive than Gz 35.

2, The lateral line grooves are much wider and deeper in Gz 15.

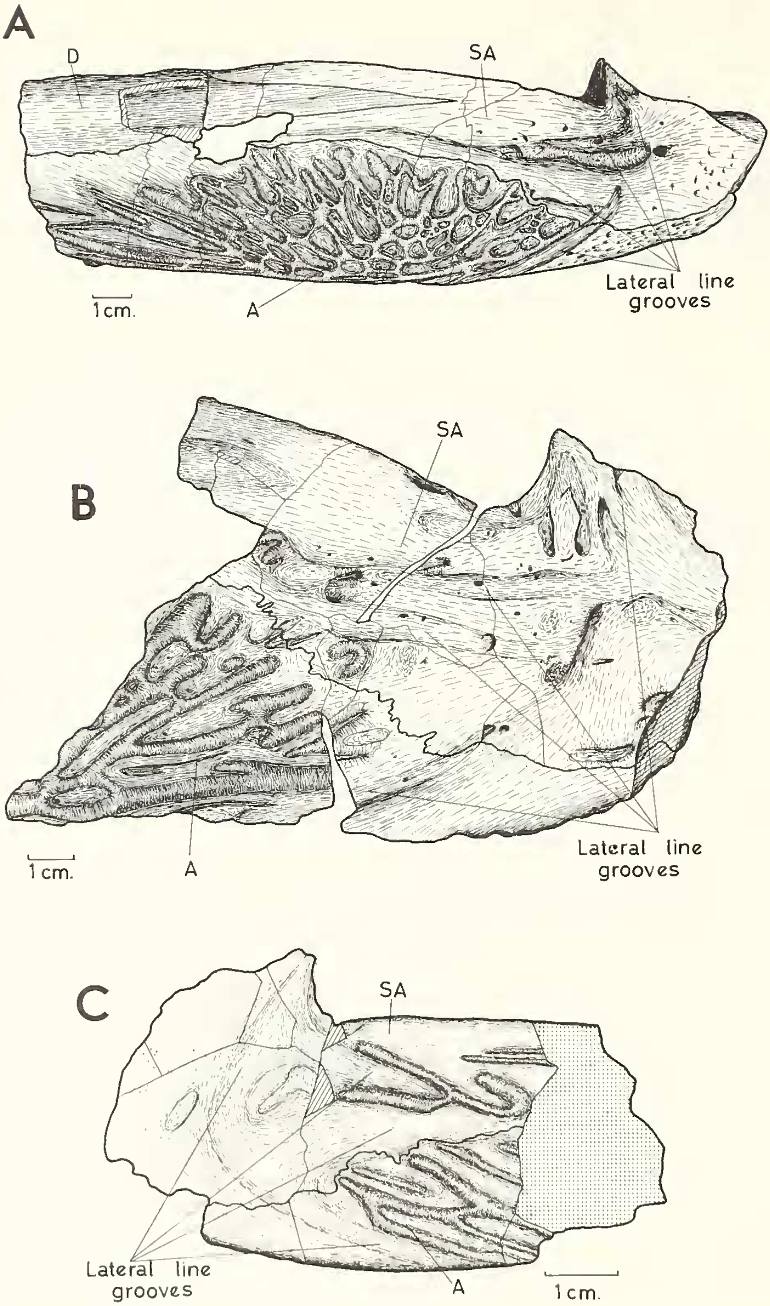
3, The ornamentation is much coarser in Gz 15.

4, In Gz 15 there is a triangular area of ornamentation posterior to the lateral line grooves on the external side of the retroarticular process.

5, The base of the jaw is much wider and more convex in Gz 15.

TABLE 2. Comparisons between lower jaws present in the material and others examined.

	B Sp 2	Gz 15	Gz 35	GSM 27964	R 4215	*P. pronus*	*P. peabodyi*	*M. jaegeri*
Size	Massive	Massive	Slender	Massive	Massive	Massive	Slender ?	Massive
Lateral lines	Shallow & wide	Deep & wide	Shallow & wide	Shallow & wide	Deep & wide	Shallow & wide	?	Shallow & wide
Ornament	Coarse & shallow	Fine & deep	Fine & shallow	Coarse & deep	Fine & deep	Coarse & deep	?	Coarse & shallow
Area of ornament external to retroarticular process	Absent	Present	Absent	Absent	Present	Absent	?	Present
Width of base of jaw	Narrow	Wide	Narrow	Narrow	Wide	Narrow	?	Wide
Shape of base of jaw	Slightly convex	Slightly convex	More convex	More convex	Slightly convex	More convex	Slightly convex	More convex
Shape of retroarticular process	Rounded	Angular	Rounded	Rounded	Angular	Rounded	Rounded	Rounded
Shape of surface of retroarticular process	Triangular + shelf	Shelf	Triangular	Triangular	Shelf	Triangular + shelf	Triangular	Triangular + shelf
Articulation	2 grooves	Saddle	2 grooves	Saddle	Saddle	Saddle	?2grooves	? Saddle
Position of chorda tympani foramen	High	Low	High	High	Low	High	High	High
Length of adductor fossa	Long	Long	Short	?	Long	Short	Short	?
Length of tooth row	Long	Short	Long	Short	Short	Medium	Medium	?
Surface of coronoid	Ornament	Ornament	No ornament	?	Ornament	?	?	?



TEXT-FIG. 15. A, specimen Gz 35, lateral view; B, specimen GSM 27964, lateral view; C, specimen BSp 2, lateral view.

6, The retroarticular process is more rounded and much narrower in Gz 35.

7, The retroarticular process has a definite dorsal surface in Gz 35 formed of a triangular hollow enclosed by ridges. No definite dorsal surface is present in Gz 15—the retroarticular process slopes smoothly from a high external edge down on to the inner side of the jaw.

8, The articulations are entirely different. In Gz 35 the articulation is limited posteriorly by a high post-condylar ridge but there is no precondylar ridge. The articulation itself consists of two parts: the lateral part is made up of a shallow trough bounded externally by the posterior extension of the lateral edge of the adductor fossa, and internally by a slightly higher ridge. This trough runs antero-posteriorly and widens anteriorly. The medial part consists of another trough at an angle to the lateral one. It is much deeper and has a V-shaped cross-section. It is bounded internally by the edge of the prearticular and laterally by the inner ridge. A possible explanation for this unusual structure is given later.

In Gz 15 the articulation is limited by high pre- and postcondylar ridges. The articulation is not in two parts but shows a normal saddle shape and is limited laterally by a low ridge of surangular. Medially it slopes gently down to the angular/surangular/prearticular suture. The prearticular here forms a horizontal shelf which is probably the base of the hamate process. The articular surface is of cartilage finished bone.

9, Because of the differing articulations the chorda tympani foramen is much lower in position in Gz 15.

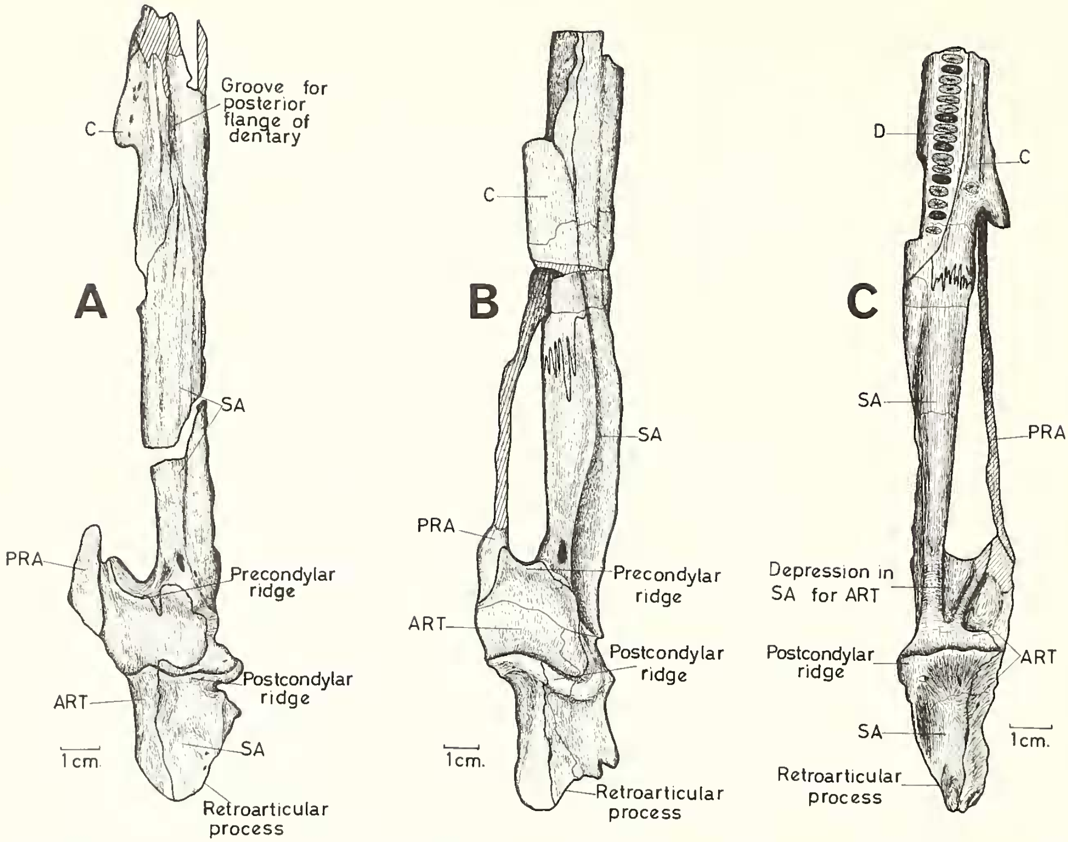
10, In Gz 15 the adductor fossa is 112·5 mm long; in Gz 35 it is 92 mm long.

11, The tooth row ends more posteriorly in Gz 35 and runs along the edge of the anterior part of the adductor fossa.

12, In Gz 15 the surface of the coronoid is ornamented by small foramina with little ridges radiating from them. In Gz 35 the coronoid has a fairly smooth surface.

13, A coronoid tooth is present in Gz 35; it is broken but fairly large. No coronoid tooth is present in Gz 15.

The specimen R 4215 is almost identical with Gz 15 and the two must have belonged to animals from the same species. R 331 and Gz 37 also appear to have come from this species. GSM 27964 and BSp 2 are very similar and they both resemble the lower jaw of *Parotosaurus pronus*. In many features, e.g. the structure of the retroarticular process and the nature of the lateral line grooves, they also resemble Gz 35. As described above, this has an unusual articular surface showing two troughs separated by a high ridge. Specimen BSp 2 has a similar articulation but no other jaws with this unusual structure have been seen. However, Welles and Cosgriff (1965) figure the lower jaw of *P. peabodyi* with an articulation made up of two troughs but do not comment upon it. Comparison with Gz 15 and GSM 27964 has suggested a possible explanation. In Gz 15 the articular is well ossified, that of GSM 27964 is less so and those of Gz 35 and BSp 2 are poorly ossified. BSp 2 probably came from a young individual as the sutures are fairly open and the ornamentation shows juvenile characters. In all four jaws the articular/surangular and articular/prearticular sutures can be followed across the retroarticular process and the latter suture can be traced on the inner side of the cotylus forward to where the articular forms the thin sheet of Meckel's cartilage lining the inner side of the jaw. However, in Gz 15 the articular covers the whole of the cotylus by overlapping the surangular labially in a thin sheet of cartilage bone. This sheet is broken laterally and the underlying surangular can be seen, its surface being covered with small ridges which held the articular in place. The articular thus forms the entire surface of the saddle-shaped articulation. In Gz 35 and BSp 2, with poorly ossified articulars, it seems likely that this sheet of articular overlapping the surangular is missing either because it was cartilaginous or because it has fallen away due to lack of ossification. Thus the normally unexposed surangular surface is visible—it has ridges corresponding with those seen in Gz 15 for securing the articular. With the hollowed-out articular on



TEXT-FIG. 16. A, specimen Gz 15, dorsal view; B, specimen R 4215, dorsal view (anterior part of specimen omitted); C, specimen Gz 35, dorsal view.

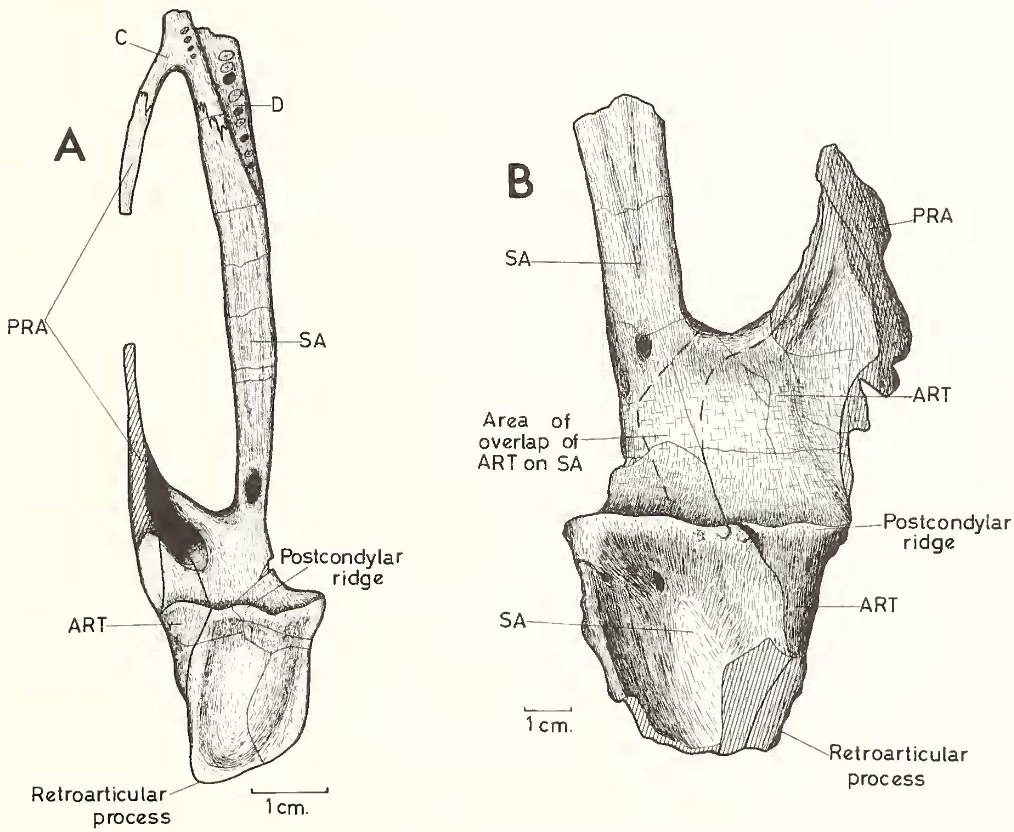
the lingual side filled with cartilage, and the surface of the surangular covered with a sheet of cartilage, the articulation would have a normal saddle shape. Possibly this has also occurred in *P. peabodyi.*

The retroarticular processes of Gz 15 and Gz 35 are very different, but GSM 27964 shows an intermediate structure although it is much closer to that of Gz 35 and BSp 2. That of Gz 15 has a high labial side which slopes steeply down lingually. The surface of that of Gz 35 is triangular in dorsal view with labial and lingual edges of equal height and with a deep triangular trough between them. Those of GSM 27964 and BSp 2 are also triangular in dorsal view but the labial side is much higher than the lingual side and there are traces of a lingual shelf present, more pronounced in GSM 27964.

Thus three types of lower jaws are represented by these specimens. Gz 35, GSM 27964, and BSp 2 appear to be fairly closely related and the latter two are similar to *P. pronus.* As parotosaurs and cyclotosaurs are very closely related—possibly some early cyclotosaurs may have had open otic notches at an early growth stage—it seems reasonable to assume that the lower jaws would not show many differences. For this reason, and also because of the inconspicuous lateral line grooves, GSM

27964 is thought to belong to a typical cyclotosaur with a skull length of about 450 mm. Gz 26 is a cyclotosaur tabular of comparable size. Specimen BSp 2 appears to belong to a smaller, juvenile individual of the same species. Gz 35 shows many slight differences and could belong to an aberrant cyclotosaur such as *Cyclotosaurus leptognathus*. Welles (1947) describes angulars assigned to the aberrant *C. randalli* which resemble Gz 35 in that the lower border is narrow with the sculpture ending close to the border, and also showing retroarticular processes with similar dorsal triangular hollows. Gz 15 and R 4215 are thought to belong to the genus *Mastodonsaurus* because: (*a*) the retroarticular processes are similar in shape to those of *M. jaegeri*, (*b*) the lateral line grooves are large and wide, and (*c*) in *M. jaegeri*, Gz 15 and R 4215, there are triangular areas of ornamentation on the external sides of the retroarticular processes.

Capitosaur postcranial material, other than from the shoulder girdle, is usually scarce. Only one fragment which could be definitely assigned to a capitosaur was found, and this was specimen Gz 1050, the head of a lumbar rib—the position in the vertebral column being indicated by the angle between the capitulum and tuberculum—from a very large animal. Shoulder girdle material is usually plentiful, e.g. at Tübingen most of the collection consists of clavicles and interclavicles. However,



TEXT-FIG. 17. A, specimen BSp 2, dorsal view; B, specimen GSM 27964, dorsal view.

only one specimen from England, in the Geology collection at Birmingham, shows the shoulder girdle in any completeness. It is not assignable as it is unassociated with skull material. The only other shoulder girdle material consists of a few fragments of the thoracic plates.

Differences between mastodonsaurs *and* parotosaur/cyclotosaurs

Mastodonsaurs	*Parotosaur/cyclotosaurs*
Anterior palatal fenestrae paired	Anterior palatal fenestra single
Lower jaw tusks protrude through dorsal surface of snout	Lower jaw tusks do not protrude through dorsal surface of snout
Ornament coarse and shallow	Ornament fine and deep
Lateral line grooves very wide	Lateral line grooves narrow
Orbital length greater than 100% of interorbital width	Orbital length less than 100% of interorbital width
Orbits large and midway along skull	Orbits small and in posterior half of skull

Mastodonsaurs can also be distinguished from advanced cyclotosaurs by the following characters:

Mastodonsaurs	*Advanced cyclotosaurs*
Choanae elongated and oval	Choanae circular
Teeth relatively small, antero-posteriorly flattened and many in number	Teeth fairly small, circular, and fewer in number
Tusks very large	Tusks moderately large
Skulls high	Skulls flattened

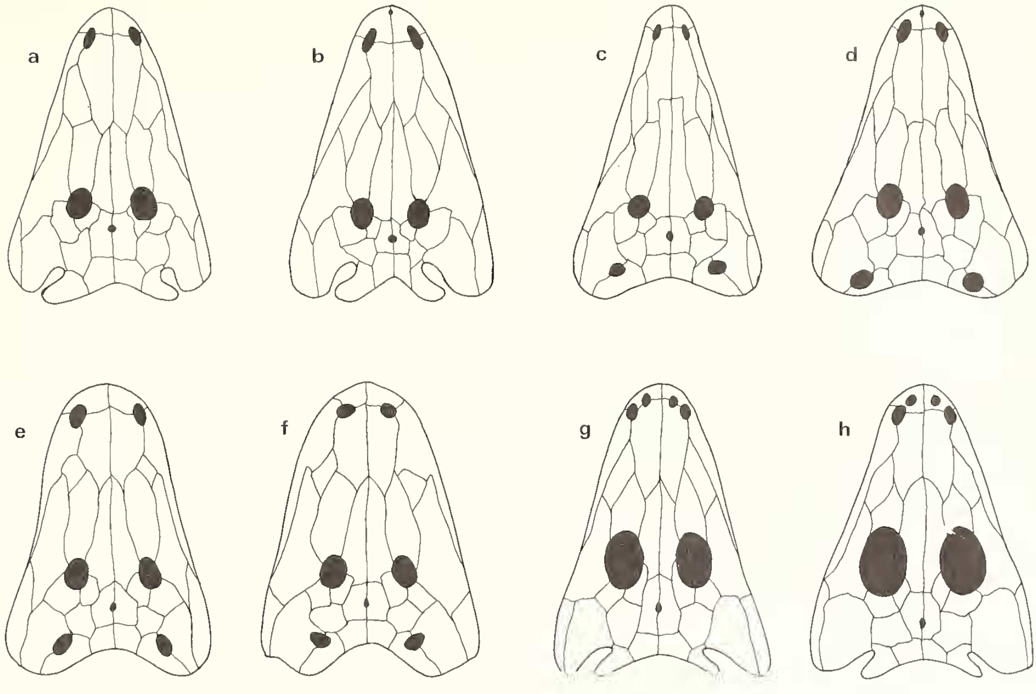
NOMENCLATURE OF BRITISH CAPITOSAUROIDS

Owen (1841) proposed the name *Labyrinthodon* as a substitute for *Mastodonsaurus* Jaeger, 1828, which he thought was inappropriate. *Labyrinthodon* is thus a junior synonym of *Mastodonsaurus*.

The type species of *Capitosaurus*, *C. arenaceus* Münster, 1836, was based upon a specimen which lacks the diagnostic postorbital region with the otic notch and thus the genus is indeterminate. As it is from the Upper Trias, it seems likely that it is a cyclotosaur. The generic name *Capitosaurus* is therefore restricted to the unique undiagnostic holotype, but the family name Capitosauridae has been retained for reasons which Welles and Cosgriff (1965, p. 8) explain.

It would be convenient to be able to use the trivial name *pachygnathus* in references to the more typical cyclotosaur represented by some of the specimens. Since Owen's 1842 paper is one of the earliest descriptions of labyrinthodont material, the species '*pachygnathus*' could only be upset and rendered synonymous if it was found to be conspecific with *Capitosaurus arenaceus* Münster (1836, p. 580). This is unlikely as the specimens show non-homologous parts and also come from different horizons. No more material is likely to come from Warwick and it therefore seems safe to refer to the material as '*pachygnathus*' and convenient to designate specimen Gz 14 as the lectotype of *Cyclotosaurus pachygnathus* (Owen) 1842 (Gz 36, Gz 13, Gz 26, GSM 27964, and BSp 2 are paralectotypes). No diagnosis can be given for this species at present, but this action has been taken in order to stabilize the nomenclature and for ease of reference.

The other cyclotosaur specimens are those which, with R 3174, are referred to one



TEXT-FIG. 18. Comparative diagram of skulls of various capitosauroids reduced to same size: a, *Parotosaurus peabodyi*; from Welles and Cosgriff (1965); b, *Parotosaurus pronus*; from Howie (1970); c, *Eocyclotosaurus woschmidti*; from Ortlam (1970); d, *Cyclotosaurus leptognathus*; e, *Cyclotosaurus posthumus*; from Fraas (1913); f, *Cyclotosaurus robustus*; from Fraas (1889); g, *Mastodonsaurus cappelensis*; from Wepfer (1923); h, *Mastodonsaurus jaegeri*; from Meyer (1844).

species of a small, primitive, and slightly aberrant cyclotosaur. They comprize Gz 38, Gz 6, Gz 11, Gz 35, and R 3174. *Diadetognathus* Miall, 1874 antedates *Cyclotosaurus* Fraas, 1889. Thus, logically but rather unfortunately as *Cyclotosaurus* is such a well-known name, *Cyclotosaurus* is a junior synonym of *Diadetognathus*. However, Miall (1874) described four specimens (syntypes) as belonging to *Diadetognathus varvicensis* without designating a holotype: Miall's no. 8 = Gz 35; 9 = Gz 37 (*Mastodonsaurus* here); 10 = Gz 18—a fragment of a left lower jaw; 11 = Gz 974—a fragment of jaw, unidentifiable as to position. Miall's specimen no. 11, Gz 974 is designated lectotype. As this specimen has no diagnostic features, *D. varvicensis* is unrecognizable from a nomenclatorial point of view and so other specimens referred to it by Miall (1874) can be transferred to different genera and species if required. This procedure enables the name *Cyclotosaurus* to continue in general use and specimens Gz 38, 6, 11, and 35, and R 3174 are assigned to *C. leptognathus* (the trivial name antedates *stantonensis*), with Gz 38 as lectotype (Miall 1874, p. 430).

It was originally intended to retain the name '*pachygnathus*' for the mastodonsaur species but Owen (1842) figured only cyclotosaur specimens as *Labyrinthodon pachygnathus*, so this was impossible. In 1876 Seeley proposed the name *L. lavisi* for the portion of lower jaw found at Sidmouth, here referred to the mastodonsaur species. The trivial name must be retained, with the lower jaw R 4215 as holotype, as *Mastodonsaurus lavisi*.

Cyclotosaurus leptognathus (new comb.) (Owen 1842)

Lectotype. Gz 38. Part of snout.
Paralectotypes. Gz 6, Gz 11, Gz 35. Cranial material plus lower jaw.
Referred specimen. R 3174—Holotype of *Cyclotosaurus stantonensis* (Woodward).
Locality of lectotype. Coten End near Warwick.
Horizon. 'Lower Keuper' Sandstone. Top of the Building Stones Formation.

Diagnosis. A small cyclotosaur with skull broad posteriorly (B:L = 80) and with slender snout (S:L = 35) and deep occiput (H:B = 22); orbits small, close together (A:OL = 75), separated by a shallow depression, situated slightly above general skull level, oval with long axis antero-posterior; frontal and jugal enter orbital margin; postorbital is anteriorly expanded; interpremaxillary foramen present; nares elongate, oval, lateral with long axis parallel to skull border, slightly elevated above surrounding skull surface; pineal foramen circular, close behind orbits; otic notch closed, post-otic bar of tabular narrow; supratemporal excluded from otic notch; posterior skull border moderately concave (index = 19); lateral line grooves narrow; ornament fine and deep.

Anterior palatal vacuity reniform; choanae elongate with long axis parallel to skull border; last premaxillary tooth large; pterygoid/parasphenoid suture short; pterygoid has facet for jaw articulation.

Foramen magnum broad, separated from supraoccipital foramen by small processus lamellosus, with entry to basioccipital foramen constricted by small processus basalis; basioccipital partially ossified; crista basioccipitalis present; slight crista obliqua on quadrate ramus of pterygoid; large paraquadrate foramen situated in quadratojugal/jugal suture.

Mastodonsaurus lavisi (new comb.) (Seeley 1876)

Holotype. R 4215. Posterior part of a right lower jaw.
Paratypes. Gz 20, Gz 9, Gz 1057, Gz 15, Gz 37, R 331, SM 369. Cranial material plus lower jaws.
Locality of holotype. Cliffs of Picket Rock Cove near Sidmouth (Lavis 1876).
Localities of paratypes. Above plus quarries in Warwickshire.
Horizon. 'Lower Keuper' Sandstone. Top of the Building Stones Formation in Warwickshire. Ten feet below the top of the Otter Sandstone and the base of the Keuper Marl in Devon.

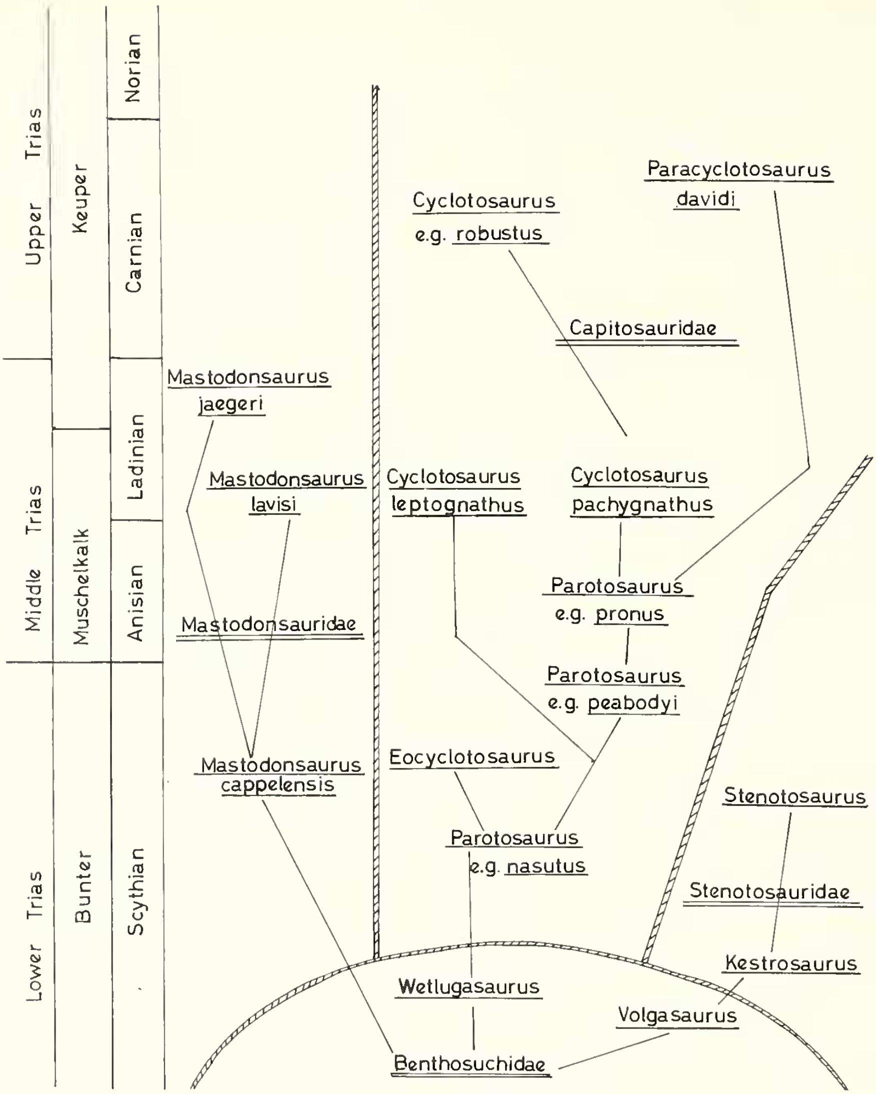
Diagnosis. A mastodonsaur with skull deep posteriorly; orbits relatively large (A:OL = 121), close together, oval with long axis antero-posterior; frontal forms large part of orbital border; pineal foramen oval with long axis antero-posterior, far behind posterior border of orbits; postorbital relatively small, unexpanded anteriorly; otic notch open with supratemporal excluded; posterior border of skull only slightly concave; lateral line grooves shallow and wide; ornament coarse and shallow.

Lower jaw massive and well ossified; retroarticular process with high lateral edge shelving smoothly down medially; coronoid toothless with radiating ridged ornament; triangular area of ornamentation on external surface of retroarticular process.

PHYLOGENY OF THE CAPITOSAUROIDEA

Romer (1966) included *Mastodonsaurus* in the Capitosauridae as did Bonaparte (1963) in his description of *Promastodonsaurus bellmani*. Bonaparte identified this species as a mastodonsaur because of: (i) the relative extension of the pterygoid/parasphenoid suture; (ii) the relative broadening of the pterygoid/parasphenoid suture; (iii) the position of the mandibular articulation with respect to the condyles. The pterygoid/parasphenoid suture is not figured so (i) and (ii) cannot be checked. However, with regard to point (iii), Bonaparte states that *Mastodonsaurus* is the only genus of capitosaur with the condyles posterior to the mandibular articulation, but this is incorrect. Those of *Parotosaurus peabodyi* are posterior to the mandibular articulation as are those of *P. birdi*, *Cyclotosaurus hemprichi*, *C. ebrachensis*, and *C. posthumus*. The palate shows an unpaired anterior palatal vacuity and, anteriorly, swollen interpterygoid vacuities. The tabular is not the typical mastodonsaur shape but is similar to that of parotosaurs with semi-closed otic notches, being slightly expanded distally; and the orbits are in the posterior half of the skull. These points suggest that *Promastodonsaurus bellmani* is probably a parotosaur with a semi-closed otic notch and fairly deep skull. Unfortunately the orbits and ornament are not preserved. Most authors remove *Mastodonsaurus* from the Capitosauridae and place it in a family of its own of equal status to the Capitosauridae and Benthosuchidae. It seems probable that the Mastodonsauridae were derived from primitive benthosuchids by the retention of some juvenile characters.

Welles and Cosgriff (1965) include only three genera in the Capitosauridae: *Parotosaurus*, *Cyclotosaurus*, and *Paracyclotosaurus*. Romer (1947) suggested that '*Capitosaurus*' *semiclausus* (Swinton 1927) should be placed in a new genus because of the exclusion of the jugal from the orbit by an anterior extension of the postorbital. Heyler (1969) has described a similar form, *Stenotosaurus lehmani*, with a completely closed otic notch. Welles and Cosgriff (1965) suggest that '*Parotosaurus*' *semiclausus* is a good ancestor for *Paracyclotosaurus davidi*. Howie (1970) emphasizes their differences, however, and suggests that *Parotosaurus pronus* is a more suitable ancestor. In fact, *Stenotosaurus semiclausus* appears to be a young individual—the zones of intensive growth are small and the sutures are very open. The distance between the edges of the tabular and squamosal is about the same as the distance between the edges of the postparietal/supratemporal suture in the middle of the skull roof so it is probable that the otic notch was effectively closed. Both *Stenotosaurus semiclausus* and *S. lehmani* lack the lachrymal flexure in the infraorbital lateral line groove. The ornamentation of *S. semiclausus* is also very different from that of cyclotosaurs and parotosaurs, consisting of very high, narrow ridges and deep, wide pits. The lateral lines are no wider than these pits. Unfortunately the ornamentation is not described in *S. lehmani*. The distinctive sculpture, paired (or nearly so) anterior palatal vacuities, absence of a lachrymal flexure, and the exclusion of the jugal from the orbit seem sufficient grounds for retaining the genus *Stenotosaurus* and for placing it in a separate family, the Stenotosauridae, as Heyler (1969) has done. This family was probably derived from a form similar to *Kestrosaurus dreyeri* (included here in the family Stenotosauridae) in turn derived from a benthosuchid like *Volgasaurus*. Swinton (1927) noted the similarity of '*Capitosaurus*' *semiclausus*



TEXT-FIG. 19. Family tree of the superfamily Capitosauroidea.

to *Kestrosaurus*. Welles and Cosgriff (1965) suggested that *Kestrosaurus* has trematosaur relationships and Heyler (1969) suggests a trematosaur relationship for *Stenotosaurus*. This resemblance seems superficial, however, and the slender snout, long vomerine plate, and paired anterior palatal vacuities indicated by these authors to show the similarity to trematosaurs can also be found in the benthosuchid *Volgasaurus* which seems a more reasonable ancestor. Text-fig. 19 shows a suggested family tree for the Capitosauroidea.

STRATIGRAPHY

Warrington (1970) has introduced formational names for the English 'Keuper' or 'Lower Keuper' Sandstone. He recognizes a 'Keuper' Sandstone Group comprising the Conglomerate Formation and the Building Stones Formation. Succeeding this, the Waterstones Formation (sometimes confusingly included in the 'Keuper' Sandstone by earlier workers) is regarded as the basal unit of the 'Keuper' Marl Group.

The Warwick and Bromsgrove specimens all come from approximately the same horizon (see Wills 1910, 1970; Walker 1969; Warrington 1970) in the upper part of the Building Stones Formation. R 3174 from Stanton is thought to come from near this horizon as well. The holotype of *Mastodonsaurus lavisi* comes from the Otter Sandstone (Warrington 1971—formerly known as the Upper Sandstone) of South Devon. Lavis (1876) said that it was collected from a level 10 feet below the base of the 'Keuper' Marl. Rhynchosaur remains belonging to a more primitive species of *Rhynchosaurus* than that found in the Midlands have also been collected from this horizon and from the base of the Otter Sandstone (Huxley 1869; Metcalfe 1884; Walker, pers. comm.). Walker (1969, 1970) therefore suggests that the South Devon horizon is older than that of the Midlands. The great similarity between the lower jaws Gz 15 and R 4215 seems, however, to contradict this, indicating that the two horizons are of closely similar age.

Cyclotosaurus is typically an Upper Triassic genus and most reported specimens come from the German Middle and Upper Keuper. Earlier specimens have been found: *Cyclotosaurus randalli* and '*Rhadalognathus*' *boweni* are from the Holbrook Member of the Moenkopi Formation of Northern Arizona and Welles and Estes (1969) assign a lower Middle Triassic age to this assemblage which also contains an ilium of *Arizonasaurus*. This resembles a poposaurid ilium from Warwick (Walker 1969), the Warwick specimen being of a more advanced type, although less advanced than similar ilia from the Upper Trias. This suggests that the English horizon is younger than the Holbrook Member. Ortlam (1970) has described a new genus and species, *Eocyclotosaurus woschmidti*, from the Upper Bunter of South Germany. This species shows some similarities to *Cyclotosaurus leptognathus*, e.g. general shape; shape and position of the pineal foramen; but the frontals do not project forwards in *C. leptognathus*, the nares are further forward, the orbits are larger, and the skull is broader generally in the latter species. *Mastodonsaurus jaegeri* is from the late Middle Trias (Lettenkohle) and the more primitive, presumably ancestral *M. cappelensis* is from the Upper Bunter of Germany. Krebs (1969) has recently argued that the upper part of the German Middle Bunter, and the German Upper Bunter are Anisian in age. He describes *Ctenosauriscus koeneni* from the upper Middle Buntsandstein of Germany as a pseudosuchian and compares it with *Hypselorachis mirabilis* from the Manda Formation of Tanzania. The latter formation is probably Anisian in age and Krebs uses the close resemblance between the two species as evidence that the German strata are also Anisian. However, the Mands Formation itself has to be dated by roundabout methods so that Krebs's suggestions cannot carry as much weight as they would otherwise do.

The stratigraphical nomenclature of the British Trias is considerably confused as the marine Muschelkalk which forms the greater part of the German Middle Trias is virtually absent in Britain. As there is no major unconformity in the middle of the British Trias, the time equivalent of the Muschelkalk must be contained in the British Bunter and Keuper, i.e. these cannot be directly equated with the German Bunter (Lower Trias) and Keuper (mostly Upper Trias).

The Middle Trias is usually divided into two stages: the Anisian and the Ladinian. The limits of these Alpine stages are not precisely known within the German sequence. Most European authorities, however, consider that the Anisian/Ladinian boundary lies within the Middle Muschelkalk, or at its top (Rieber 1967). Thus the Anisian is thought to include the Lower, and part or all of the Middle Muschelkalk, and the Ladinian is believed to include the Upper Muschelkalk and the Lettenkohle.

. Walker (1969) reviewed the reptile fauna of the 'Lower Keuper' Sandstone which comes from the same horizon at the top of the Building Stones Formation as the labyrinthodonts, and concludes that the most probable age for these beds is Early to Middle Ladinian (see Table 3) although Geiger and Hopping (1968) and more recent work by Warrington (1970) based on spore studies suggest that it is Middle Anisian or possibly even earlier. This latter result does seem very early when applied to the vertebrate evidence. The labyrinthodonts consist of a primitive mastodonsaur, a comparable German species being late Lower Trias, or possibly Anisian in age; a primitive and aberrant cyclotosaur which slightly resembles a German species from the late Lower Trias; and a more typical advanced cyclotosaur of a sort found only in Upper Triassic rocks, and resembling *Cyclotosaurus posthumus* from the Stubensandstein. Thus the labyrinthodont evidence is rather anomalous, indicating either a late Lower Triassic or an Upper Triassic age. In

TABLE 3. Stratigraphical nomenclature of the Trias.

TRADITIONAL BRITISH NOMENCLATURE (Hull, 1869)	LITHOSTRATIGRAPHICAL NOMENCLATURE: Central Midlands of England		LITHOSTRATIGRAPHICAL NOMENCLATURE: Germany	ALPINE STAGES	TRIAS
Keuper Marl	Parva Formation* Trent Formation* Edwalton Formation* Harlequin Formation* Carlton Formation* Radcliffe Formation*	Keuper Marl Group	Keuper	Norian Carnian	Upper
			Lettenkohle	Ladinian	Middle
Waterstones	Waterstones Formation		Muschelkalk		
Building Stones (Keuper Sandstone)	Building Stones Formation	"Keuper" Sandstone Group		Anisian	
Conglomerate (Keuper Sandstone)	Conglomerate Formation		Bunter	Scythian	Lower
	Hardegsen disconformity				
Bunter Upper Mottled Sandstone	Upper Mottled Sandstone Formation				

after Warrington, 1970.

* Formations defined by Elliott, 1961.

this case, greater weight is placed upon the occurrence of *C. pachygnathus* which is of a type limited so far to Upper Triassic rocks, than on the occurrence of *Mastodonsaurus lavisi* and *Cyclotosaurus leptognathus* whose close relatives have fairly long ranges. Primitive species tend to have much longer stratigraphic ranges than specialized species in the same group. Thus the earliest possible age for such a fauna seems to be late Anisian, and, taking into account the reptilian evidence, it seems much more likely that the upper part of the Building Stones Formation in Warwickshire and the Otter Sandstone in Devon is Early Ladinian (Middle Trias, Upper Muschelkalk) in age.

CONCLUSIONS

The remains of English Triassic capitosaurs are, but for the skull of *Cyclotosaurus 'stantonensis'*, very fragmentary. However, by comparison with closely allied forms with complete skulls, the remains can be placed in three groups: a primitive mastodonsaur; a primitive and aberrant cyclotosaur; and a more typical cyclotosaur. Much of the material is, however, undiagnostic and cannot be referred to any of the three species. Evidence from this and other sources shows that otic notch closure and development of the otic fenestra occurred independently many times as suggested by Welles and Cosgriff (1965). *C. leptognathus* shows an unusual method of otic notch closure as the tabular is unexpanded distally. Closure of the otic notch presumably resulted in the freeing of a larger area of the occiput leading to increased efficiency in raising the flattened skull and lowering the jaw. It seems very likely that some forms may have had open otic notches when young which closed with increasing age.

Much of the material consists of lower jaws, very few of which are described in the literature on capitosaurs. Welles and Cosgriff (1965) state that lower jaws on their own are insufficiently diagnostic to allow identification of a species. Possibly this may be the case in closely related species but the jaws studied here fall into three different and distinct categories. All show similarities in general structure as would be expected in members of the same superfamily, but the mastodonsaur jaws differ greatly from those of the two cyclotosaur species, which in turn show substantial differences from each other. The discovery and description of more lower jaws of different species may therefore show that they are more distinctive than was previously thought. Welles and Cosgriff (1965) also concluded that the only valid English capitosaur was *C.* '*stantonensis*'. It is hoped that the evidence given here satisfactorily confirms the presence of three valid species of capitosauroid in the English Trias.

The stratigraphical position of the horizon in which the labyrinthodonts are found can best be interpreted as Early Ladinian in age. This fits in well with the reptilian evidence, but spore studies at present indicate an earlier position for this horizon.

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ROBERTA L. PATON
Department of Geology
Royal Scottish Museum
Chambers Street
Edinburgh, EH1 1JF

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